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# The Study of Nephridia and Genital Ducts since 1895 (*continued*).

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With 100 Text-figures.

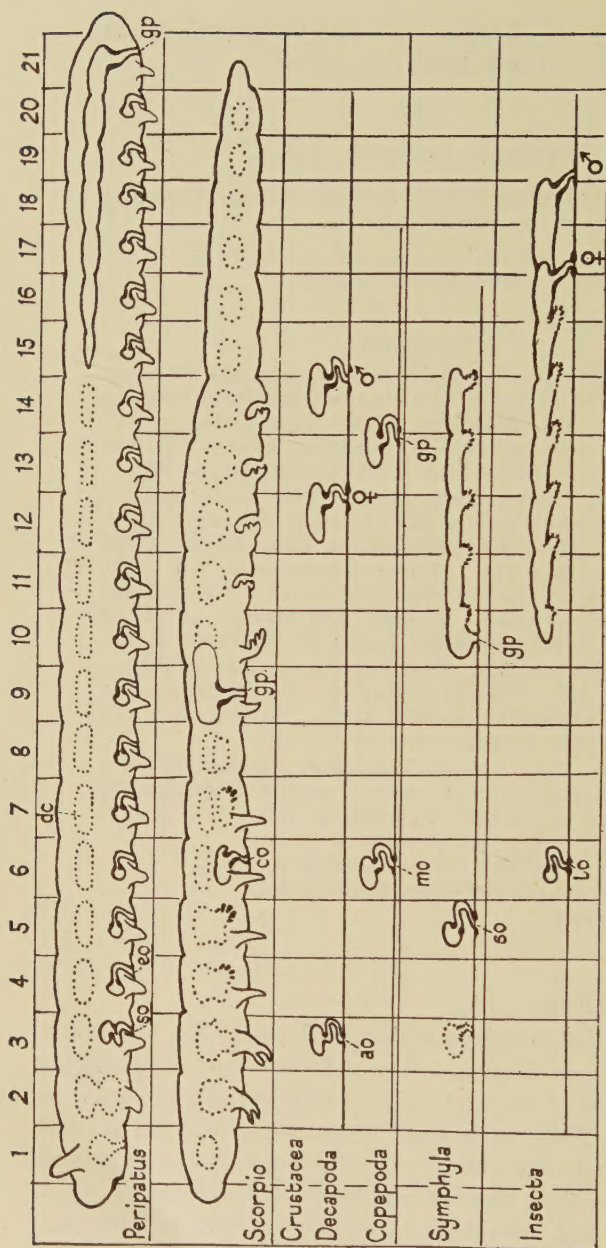
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## Phylum Arthropoda.

Before 1895 various authors (Leydig, Kowalevsky, Lankester, Sedgwick, Grobben, Weldon, Allen, and others) had compared the excretory organs of the Arthropoda to the segmental organs of the Annelida. These arthropod organs were then and are still now often called 'nephridia'. But the comparison was general and somewhat vague, since at that time the distinction between true nephridia and coelomoducts had not yet been pointed out.



TEXT-FIG. 83.

Diagram showing excretory and genital coelomoducts in various Arthropoda. Peripatus and Scorpio drawn complete, with embryonic coelomosoblastic somites and their dorsal portions in dotted line. Crustacea, Symphyla, and Insecta simplified; transient vestigial coelomoducts in dotted line. Opening of antennary organ, *ao*; of coxal organ, *co*; of excretory organ, *eo*; of lingual gland, *lo*; of maxillary organ, *mo*; of salivary organ, *so*. Dorsal coelom, *dc*. Genital pore, *gp* (both sexes indicated in Decapoda and Insecta).

In my previous review (Goodrich, 1895) the conclusion was reached that the various tubular paired segmental excretory organs and genital ducts of the Arthropoda were of the nature of genital funnels (coelomoducts). It was held that from an original complete ancestral series of such coelomoducts, still almost complete in Peripatoidea (Text-fig. 83), the condition found in the various Classes of the Phylum had been reached by the specialization of certain anterior pairs as excretory organs and the retention by certain other more posterior pairs of the primitive genital function. It was further concluded that those of the other segments, more especially of the middle region of the body, had disappeared in most Classes. These conclusions have since been very generally accepted.

But it was also stated (p. 498) 'that there are no certain traces of true nephridia in the Arthropoda'. These organs were supposed by me to have been replaced by excretory coelomoducts, or other excretory structures of different origin, such as Malpighian tubules.

Although the general conclusions mentioned above seem to hold good at the present day for the majority of the Classes of the Phylum, they may have to be revised as regards the persistence of nephridia, if not in Arthropoda in general, at all events in the Crustacea, in the light of recent research.

### Class Peripatoidea.

Of all arthropods the Peripatoidea (Onychophora) are the most instructive from the point of view of our present discussion; for it is now well known that they possess in nearly every segment of the body a pair of tubular excretory organs of typical arthropodan structure (Text-fig. 83). Each consists of a closed end-sac of considerable size, from which issues a coiled narrow excretory canal, with bladder-like enlargement leading to a short straight exit duct opening ventrally by a pore at the base of the segmental appendage (Text-fig. 84). It is remarkable in having an elongated ciliated funnel<sup>1</sup> leading from the end-sac into the canal.

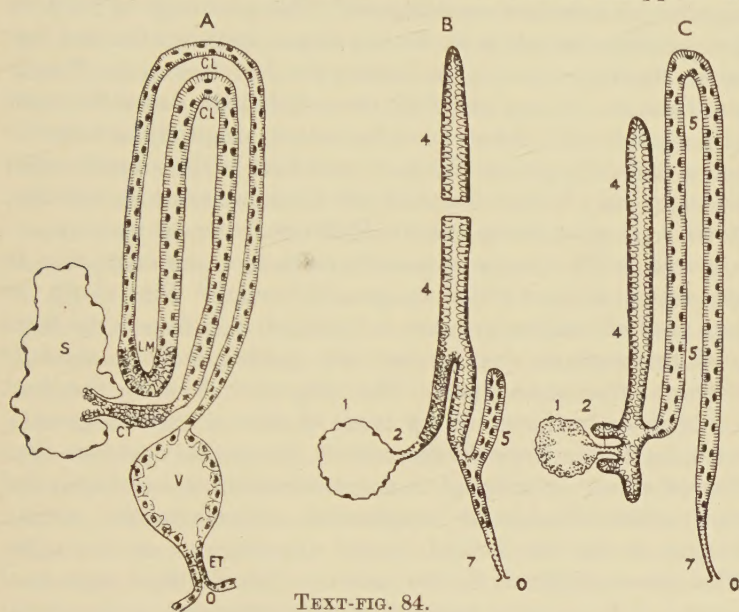
<sup>1</sup> This interesting structure (Gaffron, 1885; Dakin, 1920) is composed of ciliated columnar epithelium directly continuous with the flat coelomic

The development of these organs was studied by von Kennel (1888), and especially by Sedgwick (1888). It was shown that in every segment of the body a pair of large coelomic follicles is formed by the segmentation of the coelomesoblastic bands, the resulting somites being hollowed out, and that in the trunk segments these hollow somites become subdivided into dorsal and ventro-lateral portions. The latter grow into the developing appendages. The wall and coelom of the ventro-lateral division remains in the adult as the end-sac. From its medio-ventral wall grows a thick-walled diverticulum towards the ectoderm, the rudiment of the funnel. But, whereas von Kennel thought the canal was derived from an ectodermal ingrowth at the pore, Sedgwick described the canal as coelomesodermal and due to the extension of the funnel outgrowth to join a short ectodermal ingrowth forming the exit duct only. Von Kennel's account, however, is not convincing, and the weight of evidence is still in favour of Sedgwick's interpretation that the whole of the canal from funnel to exit duct is of mesodermal origin. No one has found a true nephridial rudiment intercalated between the exit duct and the funnel such as would justify our considering the canal as a nephridium. On the contrary, both funnel and canal appear to develop as a typical coelomoduct with a well-defined ciliated coelomostome (Goodrich, 1895).<sup>1</sup>

Good evidence that the paired coelomoducts originally were present as a complete series extending throughout the body epithelium lining the closed end-sac. Of considerable length, it leads to the excretory canal with striated excretory cells lining two regions separated by a narrow strip of granular cells, and expands to a vesicle or bladder. The excretory cells stop suddenly at the entrance into the exit duct lined by epidermal epithelium (Buxton, 1913; Zilch, 1936). The canal has an athrocytic action and takes up ammonium carminate (Bruntz, 1904). Although nitrogenous waste seems to be chiefly eliminated by the intestine as uric acid, the urine contains chloride, sulphate, phosphate, and ammonia, and the end-sac probably acts as a filter (Picken, 1936; Manton and Heatley, 1937).

<sup>1</sup> Evans (1902) studied the development of the canal in *Eoperipatus weldoni* carefully, and confirmed Sedgwick's account, concluding that the ectoderm contributes only the short duct to the exterior. Miss Glen's (1918) attempt to prove that the canal is ectodermal in origin is unsatisfactory. Her figures are inadequate, and her observations only seem to show that the exit duct is ectodermal.

was given by Sedgwick (1888), who found in the embryo rudiments in every segment of head and trunk except the mandibular, where the hollow coelomic somites disappear as



TEXT-FIG. 84.

Diagrams of A, a typical segmental organ of *Peripatus*. *CL*, striated part of canal; *CT*, coelomostome; *LM*, secretory part; *S*, coelomic end-sac; *O*, pore; *V*, vesicle; *ET*, exit duct. B, Salivary gland of *Peripatus*, and C, coxal gland of *Solifugae*. 1, end-sac; 2, coelomostome; 4, labyrinth sac; 5, striated part; 7, exit duct (Buxton, 1913).

such in late stages (Text-fig. 83). The salivary glands in the third segment, the excretory organs in the trunk segments, and the genital ducts in the last, represent the series in the adult of modern *Peripatoidea*.<sup>1</sup>

<sup>1</sup> Sedgwick's observation of a transient vestigial segmental organ, with end-sac and short canal in the antennal segment of *Peripatus capensis*, has been confirmed by Sheldon in *Peripatus novae-zaelandiae* (1888), and by Evans in *Eoperipatus weldoni* (1902), who found that the canal acquires an opening to the exterior. The modification of the organs of the third segment into salivary glands was described by Sedgwick (1888) and confirmed by Evans (1902). In the adult it opens into the buccal cavity, and preserves the end-sac, funnel, and long canal, but forms no

The genital organs consist of a pair of 'testes' or 'ovaries', situated between heart and intestine, from which issue a right and a left duct which join below the nerve-cords to open to the exterior by a median ventral pore.<sup>1</sup> This pore may be between the penultimate legs as in *Peripatus*, between the last legs as in *Peripatopsis*, or behind the last legs as in *Paraperipatus*. Sedgwick (1888) showed that the dorsal divisions of the trunk somites fuse on either side to longitudinal coelomic tubes below the pericardial floor; and that in the more anterior segments they become reduced and their cavities lost, but that in the more posterior segments (16-20 in *Peripatus capensis*) the tubes remain as paired ovarian or testicular sacs in the ventral walls of which the gonads develop.<sup>2</sup> Posteriorly the last pair of somites are not subdivided, but remain to form a continuous open duct on each side passing down to meet its fellow at the ventral pore. The outgrowth forming the duct corresponds to the excretory canal of more anterior segments. Contrary to von Kennel's description, the genital ducts are thus formed almost entirely by these mesodermal coelomoducts, and the median ectodermal invagination contributes the median vagina of the female and ductus ejaculatorius of the male. The accessory glands in the male are the modified segmental organs of the segment posterior to that giving rise to the genital ducts in *Eoperipatus* (Evans, 1902).

The general relation of the segmental organs of the adult *Peripatoidea* to the series of coelomoducts in the embryo is diagrammatically shown in Text-fig. 83.

### Class Crustacea.<sup>3</sup>

Much work has been done in recent years on the structure and development of crustacean segmental tubular excretory organs.

bladder (Buxton, 1913, Text-fig. 84). The excretory organs in the first three trunk segments tend to be reduced in the adult, while those of the fourth and fifth segments are enlarged. <sup>1</sup> The oviducts are ciliated in the region of the receptaculum seminis (Gaffron, Dakin).

<sup>2</sup> The ovisacs remain separate in *Peripatus tholoni*, are usually closely applied in the middle line, and their cavities may become confluent.

<sup>3</sup> I am greatly obliged to Prof. H. Graham Cannon, F.R.S., for very kindly reading through the proofs of this article dealing with the Crustacea.

The literature is extensive,<sup>1</sup> the results often incomplete and even somewhat contradictory; but the main conclusions may be briefly summarized as follows:

(1) The organs are all of the arthropodan type, consisting of (a) a closed hollow proximal end-sac of coelomic origin, opening into (b) a narrower excretory canal leading to (c) a distal short exit duct, of ectodermal origin, ending at the pore on the surface.

(2) Two pairs usually occur in the course of larval and adult life. They are the 'antennary gland' opening at the base of the second antenna on the third segment of the body, and the 'maxillary gland' (often called 'shell-gland') opening at the base of the second maxilla on the sixth segment (Text-fig. 88).

(3) In the Classes Branchiopoda, Ostracoda, Copepoda, Branchiura, Cirripedia, the antennary gland is the larval and the maxillary the adult excretory organ. In the lower Malacostraca it is also the case that the antennary is the transient larval and the maxillary gland is the persistent adult kidney (Subclasses Leptostraca, Stomatopoda, Syncarida, and among Peracarida the Orders Cumacea, Tanaidacea, Isopoda). But in the Order Amphipoda, and the Subclass Eucarida (Order Euphausiacea, and Order Decapoda) it is on the contrary the antennary gland which persists and the maxillary which disappears, or fails altogether to develop.

In the Order Mysidacea, however, generally considered to be the most primitive of the Malacostraca Peracarida, both glands may be present and functional in the adult, as in *Lophogaster* (Cannon and Manton, 1927).

What have been taken for vestiges of excretory organs in other segments of the body have been found in various forms. Many observers have demonstrated by the injection of coloured substances that the excretory organs have an athrocytic action: the end-sac epithelium taking up ammonium carminate and the canal taking up indigo-carminate (Burian and Muth, 1921; Bruntz, 1903-4; Vogt, 1932, and others). By such methods have been brought to light masses of athrocytic tissue at the base of appendages revealing what appear to be vestigial

<sup>1</sup> A good review of the literature is given by Waite (1899); see also Montgomery (1908), and Burian and Muth (1921).

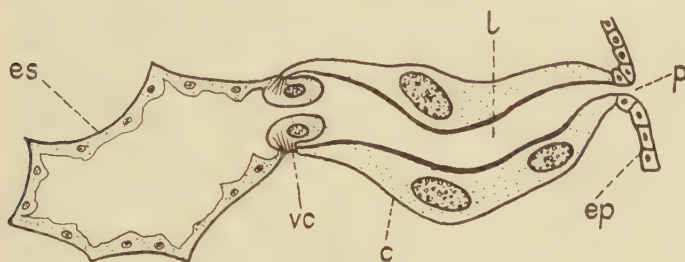
excretory organs in many segments. Generally the end-sac in the chief element remaining; as for instance in the Mysid *Praunus*, where such end-sacs are said to occur in eight thoracic segments (Vogt, 1932). Gicklhorn (1930) claims to have found a vestigial end-sac in the second segment (first antenna) of *Cyclops*, and Bergold (1910) in an Ostracod; while Miss E. A. Andrews describes a small sac and a vestige of a canal at the base of the first maxilla of *Gammarus* (unpublished) and Warren (1938) in the mandibular segment of *Artemia*. From these facts it appears that there is good reason to believe that the antennary and maxillary glands of modern Crustacea are but the specialized remnants of a once continuous series of segmental organs (coelomoducts) present throughout the body (Text-fig. 83). This conclusion is strengthened by a consideration of the position of the genital pores and ducts (see further below), which doubtless also belong to the same originally continuous series, and survive in the different groups in various positions from the nineteenth to the eleventh segment.

There remains the important question of the exact origin and homology of the excretory organs of the Crustacea. They differ much in structure—are they all of the same composition or do some of them after all contain a nephridial element? A more detailed study is necessary before attempting to give an answer.

A fully developed typical excretory organ as first clearly described by Vejdovsky (1901) and later by Nowikoff (1905), Zádavsky (1914), Cannon (1926, 1927), and others, consists of the following parts: An end-sac lined by a simple epithelium resting on an outer basement membrane, and generally attached to surrounding structures by strands of fibrous connective tissue. Immediately round the opening into the canal are a set of cells forming a sphincter or 'valve'<sup>1</sup> (Text-fig. 85). Here, on

<sup>1</sup> Although there are generally three such cells set round the opening, there may be four, as in *Gigantocypris* (Cannon, 1940) or as many as eight in some forms. The bodies of these cells projecting into the lumen of the canal act as a valve, but they also act as a sphincter owing to the presence of contractile fibrils in their base. Indeed, Vejdovsky (1901) described separate muscular cells surrounding the opening in *Gammarus* (since confirmed by Miss Andrews, unpublished). It is generally held that the valvular cells are derived from the epithelium of the end-sac, and not from the canal.

passing to the canal, the lining changes abruptly in character, the cells becoming of a clearly excretory nature. Their cytoplasm has usually radial striations peripherally and a distinct striated border towards the lumen. Special large cells may occur on the outside of the canal. This canal may be short and nearly straight or long and much coiled. The lining changes



TEXT-FIG. 85.

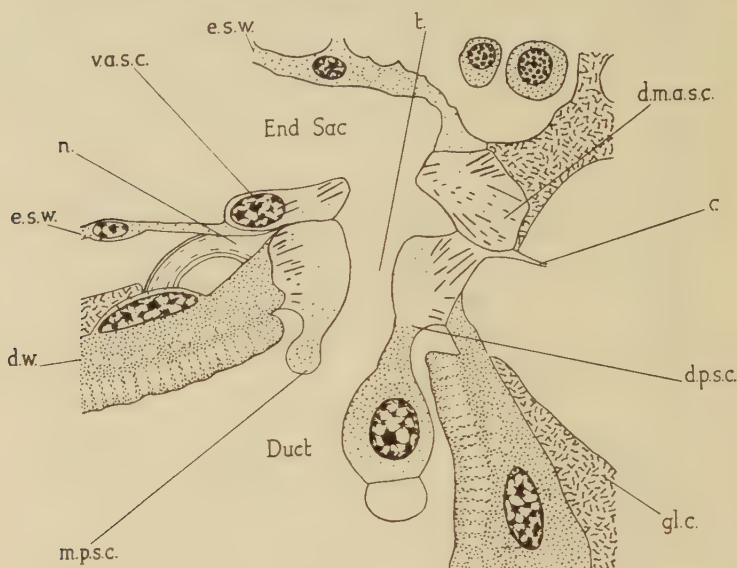
Diagram of longitudinal section through an antennary gland of a Branchiopod. *c*, canal; *ep*, epidermis; *es*, end-sac; *l*, intracellular lumen; *p*, excretory pore; *vc*, valve cell with contractile fibres.

again at the exit duct where the epithelium comes to resemble the ordinary epidermis with its covering of cuticle (various authors already quoted, and Nettowich, 1900).

It is to be noted that such a complete excretory organ is widely distributed among various genera from Branchiopoda to Decapoda, and that it may occur either in the segment of the second antenna or of the second maxilla. This full complement of parts may, therefore, be considered as that of the ancestral organ. But, various less essential parts may be lacking—the end-sac and canal remaining except where the organ is quite degenerate. On the other hand, some parts such as the end-sac and the canal may be greatly extended, specialized,

(Since this was written an excellent detailed description of the sphincter valve of the antennal gland of *Marinogammarus marinus* has been published by Mrs. M. V. Schorstein (1941). It consists of two rings of three cells each surrounding the passage from end-sac to canal. The cells of the inner ring belong to the lining epithelium of the sac and contain myofibrils. Alternating with them are the cells of the outer ring which have fibrils at their base and project far into the lumen of the canal to form the valve. The myofibrils show striations) (Text-fig. 85 A).

and differentiated, more especially in the higher forms where the distal region of the canal forms a wide thin-walled bladder.<sup>1</sup>



TEXT-FIG. 85 A.

*Marinogammarus marinus*. Section through opening from end-sac to duct of antennal gland ( $\times$  circa 1333). *c*, connexion with cuticle; *dmasc*, dorso-medial anterior sphincter cell; *dp.sc*, dorsal posterior sphincter cell; *dw*, wall of duct; *esw*, wall of end-sac; *glc*, glandular cell; *mpsc*, medial posterior sphincter cell; *n*, nerve; *vasc*, ventral anterior sphincter cell; *t*, passage from end-sac to duct (M. V. Schorstein, 1941).

<sup>1</sup> For instance, in the Mysidacea Cannon and Manton (1927) have described the wide canal of the maxillary gland of *Lophogaster* and the still more expanded canal of its antennary gland which extends both dorsally and ventrally. But it is in the Decapoda that the antennary gland reaches its highest state of complication. As Weldon (1889) first showed in *Palaemon* (= *Leander*) the bladder develops large dorsal sacs. Such 'nephro-peritoneal sacs', however, he stated rightly 'should be regarded rather as enlarged portions of a tubular system [excretory canal], such as that found in *Mysis* and in the *Thalassinidae*, than as persistent remnants of a "coelomic" body-cavity, into which tubular nephridia open' (p. 290, 1891). Nevertheless, this wise caution has been often neglected by other authors since.

It should be mentioned that the wall of the canal (and indeed of the end-sac also) appears often devoid of cell outlines being a syncytium. Of special interest is the fact that in the lower and smaller forms it usually contains only three large nuclei and the narrow lumen is intracellular from its first appearance in development (antennal gland of *Estheria* (Cannon, 1924); of *Cypris* (Cannon, 1925); and others).

The complex 'green gland' of the second antennary segment of the Decapoda has been well described more especially by Marchal (1892), Allen (1893), and Waite (1899), and by Fischer (1925), and Bruntz (1903) from the histological and physiological point of view.<sup>1</sup>

The light thrown on the morphology of the excretory organs by their development must now be considered. It is generally accepted that the end-sac represents, as in other Arthropoda, a persistent portion of the coelom of a segmental mesoblastic somite. This conclusion is in conformity with the results of Grobben, 1879; Kingsley, 1889; Lebedinsky, 1891; Allen, 1893; Boutschinsky, 1895; and Pedaschenko, 1898. These authors maintained that at least the end-sac in antennary and maxillary segments is of mesodermal origin, as opposed to the view of Reichenbach, 1877, 1886, and Ishikawa, 1885, that the whole excretory organ is ectodermal. But the most convincing evidence is that provided by Cannon (1924, 1926) in *Estheria*

<sup>1</sup> These organs differ much in detail among the various families and genera. The end-sac may have its cavity subdivided by ingrowing partitions (*Astacus* (= *Potamobius*), *Homarus*), or may give off diverticula interdigitating with those of the canal (*Palinurus*). The canal coming from the sac may have its cavity greatly subdivided to form the characteristic green labyrinth, a region formed either by subdivision of the original lumen or by the anastomosing of diverticula. A less modified region of the canal may follow between the labyrinth and the greatly expanded bladder, where the lining epithelium is smoother and covered externally with a layer of muscle, a layer of connective tissue, with blood lacunae intervening. It is the bladder which develops the remarkable lobes and chambers mentioned above, and often extending far back even into the abdomen. These may not only spread out laterally, but the right and left may join to form median dorsal sacs (*Leander*, *Eupagurus*). A short exit duct leads to the exterior at the base of each second antenna. In some this duct may form an enlarged bladder.

and Ostracods, confirmed in *Hemimysis* and *Nebalia* by Manton (1928, 1934).<sup>1</sup>

The origin of the end-sac in both antennary and maxillary glands from the coelomesoblast may now be considered as firmly established. On the other hand, the development, especially the first origin, of the excretory duct or canal is by no means so well known.

<sup>1</sup> One of the most detailed accounts of the development of an antennary gland is that of Waite (1899) in *Homarus*. He describes in the so-called late nauplius embryonic stage the rudiment of the second antenna filled with mesoderm cells. A little later a syncytial group of these cells forms the rudiment of the end-sac. Later still a proliferation inwards of ectoderm cells grows into a solid plug, which becomes applied to and partially surrounds the developing end-sac. This plug, the rudiment of the excretory canal, enlarges and acquires an intercellular lumen which opens to the exterior. At its inner end the canal rudiment fuses with the dorsal wall of the end-sac. Here an opening is pierced round which valve cells derived from the margin of the end-sac epithelium project into the lumen (at the first larval stage), and represent a temporary vestigial valve which disappears later. Thus, the valve marks the junction between mesodermal end-sac and ectodermal canal, these two parts being distinguished by the histological differences of the cells composing them. The complicated network of channels in the adult green labyrinth is said by Waite to be formed by the anastomosis of outgrowths from the canal. Woodland (1913), however, maintains that the similar network in the maxillary gland of *Squilla* is due to invaginations of the wall carrying with them connective tissue and blood spaces, an interpretation borne out by Miss Andrews's observations (unpublished) on the antennary gland of *Astacus*. An ingrowth of the epidermis at the pore gives rise to the exit duct.

Pedaschenko (1898) derived the end-sacs of the antennary glands from the third pair of distinct coelomic cavities he described in the development of the Copepod *Lernaea*. In the Branchiopod *Estheria* Cannon (1924) traced the origin of the end-sacs of the maxillary glands, and showed that they develop from the ventral region of the dorsal coelomic sacs of their segments. The end-sacs of the antennary glands he believed to be of the same origin. The canal of the antennary gland, however, he describes as of separate origin, from an ingrowth of ectodermal cells forming the syncytial wall with four nuclei surrounding an intracellular lumen which comes into secondary communication with the end-sac cavity. The valve is formed at the junction between the end-sac and ectodermal canal. In the Ostracod *Cypris* Cannon (1925) likewise finds that, while the end-sac arises in the antennary and maxillary segments from the mesoderm, the independent rudiment of the canal is formed from cells derived from the ectoderm.

The accounts given by the earlier observers mentioned above are not sufficiently detailed, precise, or complete to be conclusive; but, since 1895, Pedaschenko on *Lernaea* (1898), Waite on *Homarus* (1899), Warren on the antennary gland of *Artemia* (1938), and more especially Cannon on that of *Estheria* (1924) and on *Cypris* (1925) all (with the exception mentioned, give good evidence that the rudiments of the end-sac and of the excretory canal are at first separate and later come into secondary connexion. Moreover, Waite and Cannon, the only observers who seem to have succeeded in tracing the rudiment of the canal to its first origin, state emphatically that it comes from the ectoderm.<sup>1</sup>

It is important to note that the conclusion that the excretory organ develops from two separate rudiments, one from undoubted coelomesoderm giving rise to the end-sac and the other of more superficial origin (ectoblastic or ectomesoblastic), applies only to those antennary or maxillary glands in which the canal, whether with intracellular or intercellular lumen, is separated from the end-sac by a valvular constriction. In every case the valve marks the point where the two rudiments meet.<sup>2</sup>

Seeing, as explained above, that the canal in these crustacean excretory organs develops not from the end-sac but from a separate rudiment of ectoblastic or ectomesoblastic origin, it is tempting to compare it to a true nephridium. It has already been pointed out that most authors have adopted the theory that the canal is a 'nephridium' opening into a coelomic end-sac, since Lankester put it forward in 1885, while at the same time they ignore the distinction since drawn between

<sup>1</sup> The account by Miss Manton of the development of the canal of the antennary gland of *Hemimysis* (1928) from a separate group of cells, which grows and flattens on the end-sac into which it comes to open, probably is in agreement with this conclusion of Waite and Cannon. For, though she calls this group 'mesodermal', no conclusive evidence is given of its first origin. The same may be said of the supposed 'mesodermal origin' of the cells which produce the canal of the antennary gland of *Nebalia* (Manton, 1934).

<sup>2</sup> As already mentioned (footnote, p. 314) the valve may disappear in the later stages of development.

coelomoducts and true nephridia (Goodrich, 1895). The homology of the canal must, therefore, be re-examined from this new point of view. Cannon (1924) seems to be the only author who has discussed the subject with an appreciation of the difference between nephridium and coelomoduct, and hesitated to commit himself to the view that the canal is a nephridium (1926). The alternative he suggested that the canal is derived from an ectodermal gland seems to have little to support it.

There is much in favour of the view that the canal is nephridial in origin, when we consider the similarities in structure, function, and development between the crustacean excretory canal and the annelid nephridium.<sup>1</sup> Vejdovsky (1901) homologized the valvular apparatus with the nephridiostome; but this interpretation cannot be accepted without definite embryological evidence, for most authors consider that the 'valve' is derived from the end-sac, and we now know that an annelid nephridiostome is a part of the nephridium and developed from the same rudiment.

There remains the question whether in all the segmental excretory organs of the Crustacea the canal is of the same nature and origin. Nowikoff (1925) described the canal of the large maxillary gland of *Limnadia* as possessing an intercellular lumen opening widely into the end-sac without valvular constriction and without sudden change in the character of the epithelium. It opens to the exterior by an exit duct apparently ectodermal. Cannon (1924) had already shown that the canal of the similar maxillary gland of *Estheria* developed as an outgrowth from the wall of the end-sac, which joined the

<sup>1</sup> In this connexion it is interesting to note that Warren (1938) traced the canal rudiment in *Artemia* to a single large cell with a conspicuous nucleus, and that Miss Andrews has done the same in *Gammarus* (unpublished), and A. E. Needham in *Asellus* (1942). These cells closely resemble the nephridioblasts of Annelids. Unfortunately their first origin has not yet been convincingly described; but they may well be interpreted as ectomesodermal.

The whole question of the presence and development in Crustacea, where cleavage is so specialized, of an ectomesoderm or mesenchyme corresponding to that of Annelids is still obscure. Further study of forms with total cleavage is desirable.

ectoderm without the intervention of a separate canal rudiment. The same has been found in *Nebalia* (Manton, 1934). Cannon rightly pointed out that such a canal must be a coelomoduct. It may be compared to the coelomoducts which develop in more posterior segments to form the genital ducts.

**Summary.**—Our provisional conclusions may be summarized as follows: Paired segmental excretory organs occur in Crustacea, and consist essentially of internal end-sac, excretory canal, and exit duct. They are situated in the third (or antennary) and the sixth (or second maxillary) segments and develop early; but the maxillary gland usually alone survives in the adult lower forms, and the antennary gland alone in the adult higher forms. Vestiges of similar organs have been found in other segments, suggesting that they are remnants of an originally continuous series. In development the end-sacs have been shown to be persisting parts of the paired coelomic mesodermal somites. In a few cases (maxillary glands of *Conchostraca* and *Nebalia*) the canal, which has an intercellular lumen, develops as an outgrowth of the wall of the end-sac, and joins the epidermis to open to the exterior. Thus it arises as a coelomoduct, like the coelomoducts forming the genital ducts in more posterior segments.

Except for these few cases, the epithelium of the end-sac changes abruptly as it passes into the canal, and at this point there is a constriction and valvular apparatus (which may, however, be reduced or disappear in the full-grown organ). Such a 'valve' occurs in both antennary and maxillary glands of all the Orders, and the canal has been found to develop from a separate rudiment forming a string of cells pierced by an (at first) intracellular lumen which opens secondarily into the coelom of the end-sac. The canal rudiment is said to arise from the ectoderm in Branchiopods, Ostracods, and *Homarus*. In *Artemia*, *Asellus*, and *Gammarus* it has been traced to a single large cell, resembling the nephridioblast of Annelids, but the first origin of which is uncertain. The resemblance of these canals, especially in larval and lower forms, to true nephridia in structure, function, and development strongly suggests that they are metanephridia. If so the coelomoducts

are not developed in the segments in which the organs occur, or are very much reduced and possibly represented by the 'valve'.<sup>1</sup>

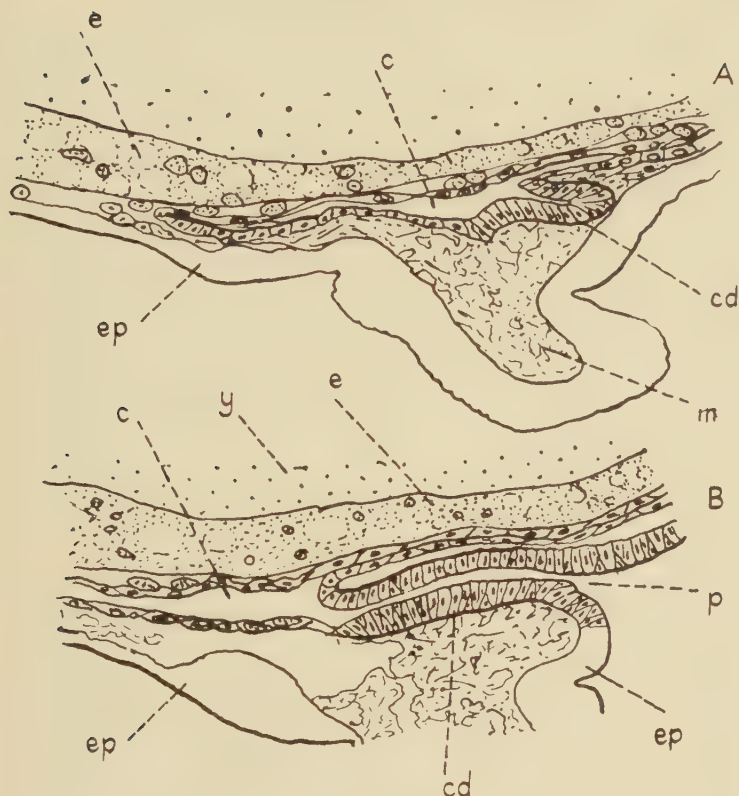
### Class Arachnida.

A pair of excretory organs, known as 'coxal glands', is present in almost all Arachnida. Opening by two ducts at the base of the fifth pair of appendages (third pair of walking legs) on the sixth segment, they are built on the usual arthropodan plan, with end-sac, excretory canal, and short exit duct (Text-fig. 84 c). In *Limulus* they are complicated by the addition of segmental elements from three more anterior segments. The canals, like the genital ducts farther back, develop as typical coelomoducts (Text-fig. 83); and the discovery by Brauer of transient rudiments of similar outgrowths in other segments is evidence that there was originally a complete series of such segmental coelomoducts.<sup>2</sup>

<sup>1</sup> If the canal be accepted as a nephridium, it might be argued that the completed organ represents a nephromixium similar to the mixonephridium of certain Polychaeta—the 'valve' being then a highly specialized coelomostome. But there seems to be no sound evidence for this view, and it is extremely unlikely that such a mixonephridium has been independently evolved in two such widely separated and different groups. There is no real resemblance between a 'valve' and a coelomostome, and for the present it is safer to consider the valve to be a special development of the Crustacea. It has already been argued that the valvular apparatus cannot be a nephridiostome.

<sup>2</sup> Well-defined coelomic sacs usually appear in all the embryonic segments. That the coxal glands are of coelomesoblastic origin was shown by Laurie (1890) in *Scorpio*, by Kingsley (1893) in *Limulus*, and by Lebedinsky (1892), who identified the end-sac, in *Phalangium*. The best account of the development has been given by Brauer (1895) in *Euscorpius*, in which four successive pairs of hollow coelomic somites (in segments 4-7) produce funnel-shaped outgrowths of the thickened epithelium of their hind walls. Only those of the sixth segment are fully developed and join the ectoderm at the base of the fifth appendages, where the pore is formed and a slight ingrowth takes place. The hollow somite remains as the end-sac, and the mesoblastic canal becomes much lengthened and coiled. The other three pairs of coelomoducts and end-sacs degenerate and disappear.

Patten and Hagen (1900) have described in detail the development of



TEXT-FIG. 86.

Transverse sections of *Euscorpius carpathicus* showing development of coxal gland at base of fifth appendage. A, Young stage; coelomoduct, *cd*, growing out of wall of coelomic sac, *c*. B, Later stage. *p*, pore pierced at point of fusion of coelomoduct with epidermis; *epc*, coelomic cavity of end-sac; *e*, endoderm; *y*, yolk (Brauer, 1895).

the large coxal gland of *Limulus*. Here the canal also develops as a coelomoducal outgrowth in the sixth segment; but in addition segmental rudiments of end-sacs appear in segments 2-5 and 7. Those corresponding to the chelicerae (segment 2) and to the fourth walking legs (segment 7) disappear. The four remaining rudiments on each side form the four lobes of the adult organ. The end-sacs develop branching diverticula which, together with strings of mesoblastic cells attached to them, form a complex

These results of Brauer on the development of the coxal glands in *Euscorpium* have been confirmed in other and more specialized groups of Arachnida; but they do not always belong to the same segment, and there may be more than one pair: indications that the adult organs are survivals of a once continuous series.<sup>1</sup>

Just as in *Peripatus*, so in the Arachnida, the genital ducts develop as coelomoducts. They occur in the ninth (second abdominal) segment. The somites in this genital segment unite dorsally to form (with contributions from other segments) the median gonadial sac, and grow down on each side of the alimentary canal to join ventrally a median ectodermal ingrowth at the genital pore (Brauer, 1895; Purcell, 1895; Kautzsch, 1910).

#### Classes Chilopoda, Chilognatha, Symphyla, and Insecta Hexapoda.

Coelomoducts seem to be rarely represented in these terrestrial Arthropoda, where the excretory function has been so much assumed by the Malpighian tubules of quite different origin.

system of tubules (in the lobes, and canals joining the lobes to each other and the basal region of the posterior end-sac) leading into the excretory canal.

<sup>1</sup> They belong to the sixth segment (third pair of walking legs) in Scorpionidea; the fifth segment (second pair of walking legs) in Hydrachnidae among Acarina; the fourth segment (first pair of walking legs) in Pedipalpi, Phalangidea, and Araneidea (of the Suborder Dipneumones): and even open in Solifugae near the palps, second appendages of the third segment (Sturany, 1891; Buxton, 1913). In *Koenenia* they open between the second and third appendages (Rucket, 1901). Moreover, Buxton (1913, 1917) has shown that in the Araneidea (Suborder Tetrapneumones) each coxal gland has two end-sacs joined by a common canal, but opening by two exit ducts, one at the base of the first and the other of the third walking leg; also that in *Thelyphonus* the gland has two end-sacs of which the ducts unite to open at the base of the first walking leg, and that in the Pedipalp *Charon* there are two separate pairs of sacs and canals, the first opening as usual on segment 4 and the second on segment 6.

Embryonic vestiges of a second pair of coxal glands are said to occur in Pedipalpi in the fifth segment (Pereyaslawzewa, 1901; Gough, 1905; Schimkewitsch, 1906).

They persist, however, as genital ducts and sometimes as 'head' or 'salivary glands'.<sup>1, 2</sup>

In all these four Classes the general course of the development of the genital organs is much as in the Peripatoidea. The trunk somites of Chilopoda (Heymons, 1901), Symphyla (Tiegs, 1940), and Insecta (Wheeler, 1893; Heymons, 1892) become subdivided, and their consecutive dorsal lobes in a varying number of segments fuse into two longitudinal tubes below the pericardial floor. The germ-cells may be precociously segregated, but sooner or later are found in the walls of those segmental coelomic sacs which combine to form the paired or median ovisacs or testis-sacs (so-called ovaries and testes) above the gut. The Diplopoda apparently differ from the foregoing in that the genital lobes of the somites meet and combine to form a median ovarian or testicular sac below the gut (Heathcote, 1888).

A pair of coelomoducts may grow out of each pair of the genital coelomic sacs, as described by Wheeler (1893) in Orthoptera; but only a posterior pair develop fully and join the

<sup>1</sup> The paired 'salivary glands' of the Chilopoda, related to the second maxillae, and provided with canals and end-sacs, are probably modified arthropodan segmental organs (Herbst, 1891; Fahlander, 1938). Also the labial glands of the Chilognatha, which long ago were shown by Heathcote (1888) to develop as end-sacs and coelomoducts from the third pair of mesodermal somites.

Recently Tiegs (1940) has given a detailed account of the development of the salivary gland of the Symphyliid *Hanseniella* from the maxillary somite (fifth segment). The whole duct of the gland is formed as a coelomoduct from the lateral part of the somite which gives rise to the end-sac. Tiegs also has described a similar but transitory larval segmental organ which develops from the premandibular somite (third segment).

Some at least of the tubular 'head glands' of Insecta seem also to be segmental organs. Such are the 'salivary glands' of Thysanura and Collembola (Nassonow, 1886; Hoffmann, 1904). Bruntz (1904) has shown that their end-sacs eliminate ammonium carminate and their canals indigo-carminate.

<sup>2</sup> Snodgrass, in his interesting work on the insect abdomen (1936), gives an essentially correct account of the morphology of the gonadial sacs and their ducts in Arthropods; but it is unfortunately somewhat confused by his retention, both in text and in figures, of the name 'nephridium' for structures which he admits are (and also names) coelomoducts.

ectoderm ventrally to form the adult oviducts or sperm-ducts. Almost invariably the genital pore is median, and here from an ingrowth of ectoderm develop the median genital duct and structures related to it (Metcalf, 1932; *Insecta* and literature). The more anterior vestigial coelomoducts disappear (Text-fig. 83).

### Summary for Arthropoda.

From the account given above of the structure and development of the excretory organs and genital ducts it may be concluded that there is good evidence: (*a*) that they are derived from a continuous series of paired segmental organs originally present in every segment of the body; (*b*) that there has been an increasing tendency in the various Classes for these organs to become reduced in number in the adult, and specialized as 'salivary' glands in the head region, excretory glands in the mid-trunk region, and genital ducts in the more posterior region; (*c*) that the evidence for original continuity rests on their survival in almost all the adult segments in *Peripatus*, their full development in several larval or adult segments in Crustacea; and also the varying position of the few that do persist in the most specialized groups; (*d*) also in the appearance in the embryo of vestiges in all or many segments which lack segmental organs in the adult. It may further be supposed that in the primitive ancestor the whole series of organs was more uniform not only in structure but also in function.

It is probably owing to the excretory function having been assumed by some of the coelomoducts that the segmental nephridia have so completely disappeared in Arthropoda; though traces of them may perhaps be represented in the canal of the excretory organs of Crustacea, in those cases where the canal develops separately from the end-sac, and opens secondarily into it.

Further specialization may lead to the replacement of excretory coelomoducts by new renal organs derived from the wall of the alimentary canal (Malpighian tubules of terrestrial forms).

The arthropodan segmental organs are peculiar in that, in accordance with the haemocoelic character of the general body-cavity, they do not open into it, but into a closed end-sac ('salivary' and excretory organs) or into a genital sac ('testis' or 'ovary') of coelomic origin, and derived from the embryonic somite. These segmental coelomesoblastic somites become subdivided each into a more dorsal and a more ventral portion, except in the most anterior and most posterior segments. From the wall of each ventral chamber develops a coelomoduct as a centrifugal outgrowth which usually joins the ectoderm and opens ventrally to the exterior. These coelomoducts represent the primitively complete paired segmental series, seen almost uninterrupted even in the adult Peripatoidea, but reduced in number and specialized in the various divergent Classes. The dorsal portions of a varying number of the more posterior somites join to form paired longitudinal genital coelomic sacs opening to the exterior by the posterior coelomoducts which retain their original function as genital ducts. But the ventral portions of the other segments gradually take on new functions. Thus, in the trunk region they become excretory, and in the head region they may become converted into so-called salivary glands. The characteristic closed end-sac of these organs is derived directly from the ventral portion of the somite of its segment, while the coelomoduct forms the glandular canal, often with the addition of an exit duct formed by ectodermal ingrowth at the pore.

In the Arachnida, Chilopoda, Chilognatha, Symphyla, and Insecta Hexapoda no trace of a true nephridium has been found, either in the embryo or in the adult. Although it has been suggested that such a nephridial element occurs in *Peripatus* (p. 306, note 1), no good evidence of its presence has yet been brought forward. It is only in the Crustacea that there has been found intercalated between the coelomic and ectodermal (exit duct) rudiments a third rudiment which may possibly represent a nephridial element forming the excretory canal itself. However, even in the Crustacea, not only does the genital duct appear to be formed entirely by the combination of a coelomoduct with a short epidermal ingrowth at the pore, but also the

excretory canal of the maxillary gland in *Estheria* and *Nebalia* (p. 313) appears to be coelomoducal.

In the majority of cases in which the development of the canal of the antennary and maxillary glands of the Crustacea has been described in detail it has been found to arise, not as an elongated outgrowth of the end-sac but from a separate rudiment probably of ectoblastic or ectomesoblastic origin. This rudiment grows so as to join the end-sac to the epidermis, and acquires a lumen leading from end-sac to pore. A canal so formed, composed of few large cells and with a usually intracellular lumen, often strikingly resembles the larval nephridium of an Annelid or Mollusc; and in *Gammarus* and *Artemia* it has been traced in development to a single large cell recalling the nephridioblast of an Annelid. But it always comes to open secondarily into the end-sac, much as the metanephridium opens into the annelidan coelom. A special valvular apparatus marks the junction of the canal with the end-sac, and may represent not the nephridiostome as often suggested but the reduced coelomostome.

If the third element mentioned above is indeed a nephridial rudiment, and if the interpretation just suggested is correct, we should have in this crustacean excretory gland a compound organ closely resembling the mixonephridium of the Polychaete. But more evidence is required before such a view can be accepted, and the resemblance is probably due not to direct homology, but to the opening of the nephridium into the coelom having been independently acquired in Crustacea and Annelida. The result might be similar in the two cases.

### Phylum Mollusca.

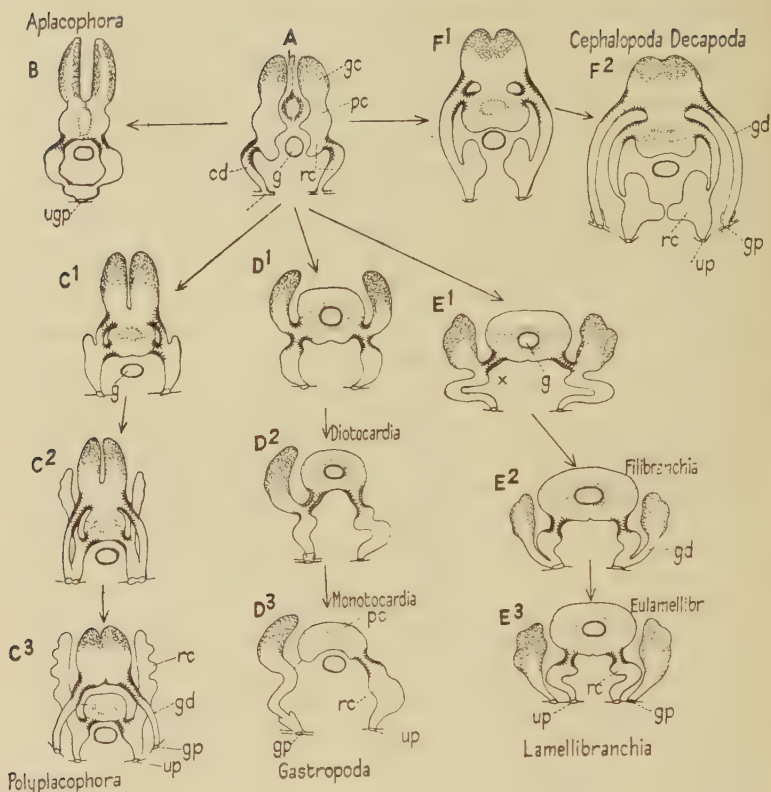
The Mollusca, in spite of their great diversity of structure in adaptation to various modes of life, are all built on essentially the same plan as regards their excretory and reproductive organs. In the adult stage they are provided with a pair (sometimes apparently with two pairs) of tubular organs leading from the coelomic cavity to the exterior posteriorly. Comparison of these organs in the various groups of the Phylum shows that they represent the original genital ducts, and still function as

such in the more primitive forms, but that they have gradually acquired the excretory function and become more or less specialized as kidneys. This may lead to their subdivision and the formation of separate renal and genital ducts to the exterior.

By the older authors these paired organs were freely compared to the excretory organs of Annelids and called 'nephridia'. In 1895 (Goodrich, 1895) it was maintained that the real nephridia of Molluscs are represented by the paired kidneys in larval stages, and that the excretory organs of the adult are derivations of the coelom, homologous with the 'genital funnels' of Annelids, and comparable to what we now call the coelomoducts of Triploblastica in general.

Quite briefly the history of these organs in the Mollusca seems to have been as follows (Text-fig. 87): Originally there was a pair of coelomic cavities (Text-fig. 90) which met above the gut to embrace the dorsal blood-vessel (heart). From their walls developed the gonads whose products were carried out at maturity by a pair of coelomoducts opening to the exterior posteriorly. These coelomoducts also tended to assume the function of carrying out excretory products, and became the adult renal organs. At the same time the earlier larval nephridia and other embryonic excretory organs (p. 331) disappeared in the course of development. Meanwhile the originally simple and continuous coelomic cavities tended to become differentiated into three chambers: (1) a central sterile portion which combined with that of the opposite side to surround the heart and probably also the gut, and is known as the pericardial coelom; (2) an antero-lateral portion, the special gonadial coelom; (3) a posterior renal coelom, apparently formed from the enlargement of the coelomoducal outgrowth itself, and serving for the passage of both excretory and genital products. This renal coelom formed the adult kidney or organ of Bojanus, while the primitive protonephridium became restricted to the larval period (Text-fig. 86).

The general interpretation of the morphology of the excretory and genital organs of the Mollusca put forward by me in 1895 has since been accepted by such authorities as Lankester (1900), Pelseneer (1906), Naef (1913), and others.



TEXT-FIG. 87.

Diagram showing specialization and subdivision of coelom and coelomoducts in Mollusca. A, Primitive plan. B, Aplacophora. *cd*, coelomoduct; *g*, gut; *gc*, gonadial coelom; *gp*, genital pore; *pc*, pericardial coelom; *rc*, excretory renal coelom; *ugp*, urino-genital pore; *up*, excretory pore. Along line c coelomoduct becomes split from coelomostome outwards and genital coelom closed off. Along line d (Gastropoda represented as untwisted) both heart and pericardial chamber may surround gut, and left genital chamber comes to open into renal and left coelomostome may be closed, left coelomoduct remaining as genital duct. Along line e gonadal chamber comes to open into coelomoduct which may become split into separate excretory and genital ducts. In line f coelomoduct also becomes split into two, and generally they are asymmetrically developed.

This view, outlined above, that the renal organs are coelomoducts was founded on both the comparative anatomy and embryology of representatives of all the Classes of the Phylum. It has been clearly shown that in all Molluscs the tripartite coelomic cavities originate in paired masses of coelomesoblast which become hollowed out.<sup>1</sup> They correspond to the paired coelomesoblastic bands of Annelids, and may be considered as a single pair of somites from which grow out a single pair of coelomoducts. As in Annelids these somites are in most cases, if not in all, the products of the division of two primary coelomesoblast cells derived in early cleavage from macromere D.<sup>2</sup>

Meisenheimer (1898, 1901 *a* and *b*), however, maintains that in *Limax*, *Dreissensia*, and *Cyclas* the coelomic rudiments are derived rather late in development from proliferations inwards of superficial cells, and are therefore ectodermal in origin. Otto and Tönniges (1906) and Dautert (1929) also believe that in *Paludina*, where no mesodermal teloblasts can be seen, the coelomic rudiments are formed from cells proliferated from the ventral 'ectoderm'. These unorthodox

<sup>1</sup> Among the more recent describers of the paired coelomic rudiments may be mentioned: Higby and Heath (1912), and Hammarsten and Runnström (1925) in *Chitonidae*; Drummond (1902), and Otto and Tönniges (1906) in *Paludina*; Carr Saunders and Poole (1910) in *Aplysia*; Meisenheimer (1901 *a*) in *Dreissensia*, and (1901 *b*) in *Cyclas*; Herbers (1913) in *Anodonta*; Faussek (1900) in *Loligo*.

<sup>2</sup> We are not here concerned with the detailed description of cleavage and cell-lineage; but it may be pointed out that, in the majority of species studied, the paired teloblasts which give rise to the coelomesoblastic bands destined to form the coelomic rudiments (= one pair of somites) are directly or indirectly derived from the macromere of quadrant D. According to Smith (1935) in *Patella* and Crofts (1938) in *Haliotis*, cell D divides directly into the two mesoteloblasts. Usually the two mesoteloblasts result from the equal division of the fourth quartette cell 4*d*, or from its daughter cells after the elimination of endoderm cells: Heath (1899) in *Ischnochiton*, Robert (1902) in *Trochus*, Conklin (1897) in *Crepidula*, Wierzejski (1905) in *Physa*, Holmes (1900) and Pötzsch (1904) in *Planorbis*, Lillie (1895) in *Unio*, Herbers (1913) in *Anodonta*. The actual derivation of the coelomic rudiments from the mesoteloblasts is described in *Chitonidae* by Higley and Heath (1912), in *Physa* by Wierzejski (1905), in *Aplysia* by Carr Saunders and Poole (1910), in *Anodonta* by Herbers (1913).

interpretations are possibly due not to errors of observation but to the misuse of the term 'ectoderm' when applied to a specialized mode of segregation of the germ-layers.<sup>1</sup>

There remain further points of interest to consider: what is the evidence that the definitive renal organs are coelomoducts, and if so how is it that the gonadial coelom comes, in some cases (Gastropoda, Lamellibranchia), to open directly into this renal cavity, and finally is there reason to believe that some Mollusca (Polyplacophora, Cephalopoda) retain traces of having been derived from ancestors with two or more segments?

That the kidneys of the adult are indeed coelomoducts that have taken on the function of excretion (Goodrich, 1895), and are not merely chambers of the coelom more or less partitioned off, is shown by their development as outgrowths from the coelomic wall (in *Acanthochiton*, Hammarsten and Runnström, 1925; in *Paludina* and *Bithynia*, v. Erlanger, 1891, 1892; and other cases). The process of the formation of a thickening of the coelomic epithelium, of its outgrowth as a funnel-shaped process, of the narrowing of the coelomostome to form the reno-pericardial funnel, has been described in detail by Drummond (1902), and by Otto and

<sup>1</sup> In defining germ-layers both the origin and the fate of the cells must be considered. If we look upon cleavage as a process leading to the gradual sorting out of the different building materials, the names ectoderm, mesoderm, and endoderm should not be applied to a cell or group of cells until the segregation of the material in it has been completed. Thus a cell derived from macromere D should not be called mesodermal until it has been cleared of its endodermal component, a process which it may take several divisions to accomplish. Moreover, the germ-layer character of a cell does not depend merely on, and cannot be defined by, the position it occupies in the embryo. If traced back far enough, not only the ectoderm but all the germ-layers are found on the outer surface; this is obvious in the case of a hollow blastula. In Annelids the primary coelomesoblast (4*d*) may be retained for a time in the wall of the gut. There seems to be no reason why, in certain Molluscs, it or its derivatives should not be associated with ectodermal material in the superficial layer of cells, from which it might later be segregated in the process of proliferation described by Meisenheimer and Tönniges. The origin of the coelomesoblast in the form of enterocoelic pouches described in *Paludina* by Erlanger (1894) and Fernando (1931) is doubtless founded on erroneous observations.

Tönniges (1906) in *Paludina*. Also the growth of the distal end to meet an ectodermal invagination at the pore.<sup>1</sup>

But, if the reno-pericardial funnel represents the original coelomostome, the genital products should first be shed into the coelom and then carried out by this funnel—as they still are in *Solenogastres*. The passage of these products directly into the coelomoduct canal may perhaps be explained as a secondary modification due to the gonadial chamber coming to open into the coelomostome itself, and then farther and farther down the coelomoduct towards the external pore.<sup>1</sup>

Thus, in the more primitive *Gastropoda*, such as the Order *Aspidobranchia*, the genital products may be discharged into the definitive right kidney or its reno-pericardial duct.<sup>2</sup> The adult right pore is, then, a urinogenital pore. But, in the Order *Pectinibranchia* and the *Neritacea* the definitive right kidney is no longer present as an excretory organ, loses its reno-pericardial opening, and serves only to contribute to the formation of the genital duct. The adult right duct thus becomes again purely genital, as was probably the original coelomoduct in the remote ancestral *Mollusc*. In these advanced modern forms, however, a considerable length of the duct with its specialized parts is derived from the ectodermal ingrowth at its pore (Text-fig. 87).

A somewhat similar modification seems to have occurred in *Lamellibranchia*, leading to the separation of the genital and renal outlets (Pelseneer, 1891; Goodrich, 1895). In the more primitive *Protobranchia* the genital products are discharged into the coelomoduct (kidney) near its renopericardial funnel, then nearer the external pore as in *Pecten*, and finally the genital duct comes to open separately as in *Anodonta*.

<sup>1</sup> This explanation is suggested by the comparative anatomy of adults, and supported by embryology. Drummond (1902) and Otto and Tönniges (1906) have clearly shown how the genital chamber of the coelom in *Paludina* comes to open into the coelomostome of the small right kidney, which closes off from the pericardial coelom to form the duct leading to the distal region derived from the ectoderm of the mantle cavity.

<sup>2</sup> No *Gastropod* is known with paired gonads. B. Haller seems to have been mistaken in describing such a condition in *Puncturella* (*Cemoria*); see Pelseneer (1898) and A. Meyer (1913).

Pelseneer (1906) and Odhner (1912) came to the same conclusion.

Coming now to the question of segmentation in the Mollusca: Pelseneer (1898, 1906) pointed to the presence of an anterior pair of genital and a posterior pair of excretory ducts in both Polyplacophora and Cephalopoda as evidence of descent from an ancestor composed of two segments, and this theory has been further developed by Naef (1926) in his interesting work on the general morphology of the Mollusca. While admitting that there is something to be said for the theory that they have been derived from metamerically segmented ancestors, the apparent absence of any true segmentation of the coelomesoblast in the embryo of any Mollusc is a serious objection urged against it. On the whole, it seems more probable that the Mollusca diverged from the annelidan stem before metameric segmentation had become established,<sup>1</sup> and that the duplication of certain organs in Polyplacophora and Cephalopoda is due to the tendency towards the repetition of parts already so conspicuous in *Platyhelminia* and *Nemertina*.<sup>2</sup>

<sup>1</sup> Many resemblances in cleavage, larval development, and adult structure point to a relationship between Annelida and Mollusca. However, while it is unnecessary to assume that the Molluscs are derived from segmented Annelids, there is good reason to believe that both groups have diverged from a common ancestor not yet fully segmented, but which possessed a larval stage of the trochophore type and a pair of coelomic cavities and coelomoducts in the adult.

<sup>2</sup> It is unnecessary here to enter in detail into the long controversy about the origin and homology of the single pair of ducts in Solenogastres and the corresponding renal pair and additional genital pair of ducts in Polyplacophora. Both pairs appear to develop as coelomoducts (Higley and Heath, 1912; Hammarsten and Runnström, 1925) which meet ectodermal ingrowths to open to the exterior. They may be considered either as the result of duplication or, as suggested by Hoffmann (1930), as due to the splitting from within outwards of the original pair of coelomoducts (by a process similar to that described above in *Lamellibranchia*) accompanied by the closing off of the anterior genital coelom, and thus avoiding the passage of the genital products through the pericardial chamber. The suggestion of Plate (1901), severely criticized by Soderström (1925), that the gonoduct is a secondary ectodermal ingrowth is clearly untenable.

The separate gonoducts in Cephalopoda, shown by Döring (1908) to develop as outgrowths of the wall of the genital coelom, may also

### Development of Larval Protonephridia.

A pair of larval excretory organs of nephridial nature have been found in some Gastropoda (Prosobranchia and Pulmonata) and Lamellibranchia.<sup>1</sup> In 1895 I maintained that they are the only true nephridia occurring in the Mollusca. That they are protonephridia comparable to those of larval Annelids, and homologous with the protonephridia of other groups is now generally admitted (Fage, 1906; Meisenheimer, 1909; Willem, 1910; and many others). The earlier observers, whose observations were mostly incomplete, described them sometimes as closed and sometimes as open internally, and traced their origin sometimes to ectoderm and at other times to mesoderm or mesectoderm.<sup>2</sup>

The best modern work on these organs in Pulmonata is that of Meisenheimer (1898, 1899, 1901). He showed that in the

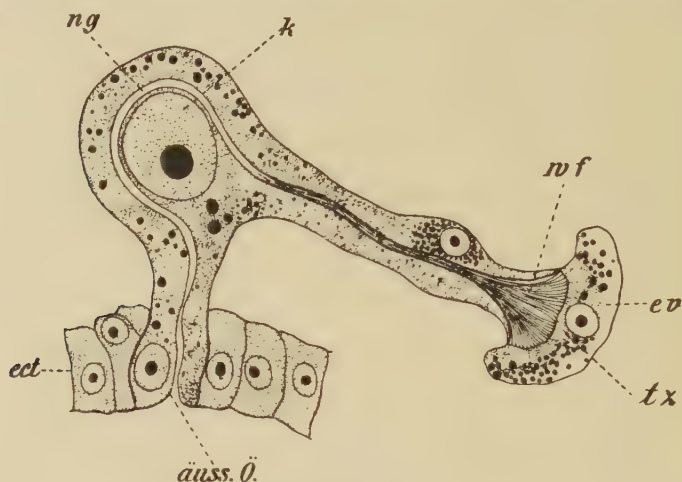
be considered as due to secondary duplication and splitting (Text-fig. 87).

Thiele (1902), believing that the genital sacs and paired ducts of the Solenogastres represented the gonads and gonoducts of a Platode-like ancestor, came to the extravagant conclusion that there is no true coelom in these Molluscs. Since then Odhner (1921), Nierstrasz (1922), Sarvaas (1933), and Hoffmann (1937) have also maintained that the Mollusca in general have no true coelom! But it is clear that far from Thiele's view of the homology of the sacs and ducts in Solenogastres being opposed to the Gonocoel theory it is really in its favour, the foundation of the theory being that the coelom and coelomoducts of the Coelomata have been derived in phylogeny from the gonads and their ducts in the lower forms.

<sup>1</sup> They have often been confused with certain external ectodermal excretory cells found in the embryonic and larval stages of many Molluscs, more especially in Opisthobranchia, which seem to have nothing to do with nephridia (Mazzarelli, 1904; Casteel, 1904; Glaser, 1905; Carr-Saunders and Poole, 1910; Heymons, 1893; v. Erlanger, 1893).

<sup>2</sup> Larval nephridia have been described by Batrahli, 1877, v. Erlanger, 1891, 1892, in *Paludina*; Rabl, 1879, Fol, 1880, in *Planorbis*; Rabl, 1879, Wolfson, 1880, de Meuron, 1884, Jourdain, 1884, P. and F. Sarasin, 1882, in various Pulmonata; Hatschek, 1880, in *Teredo*; Ziegler, 1885, in *Cyclas*. They were considered to be of ectoblastic origin by Fol and Wolfson; mesoblastic by Rabl and Hatschek; both mesoblastic and ectoblastic by v. Erlanger. More recently their structure, function, or development are dealt with by Meisenheimer (1898, 1899, 1900, 1901, 1909), Stauffacher (1898), Willem (1910), and Wierzejski (1905).

Pulmonata Basommatophora (Ancylus, Physa, Planorbis, Limnaea) the protonephridium consists of a syncytium pierced by an intracellular lumen without cilia (Text-fig. 88). The outermost part, with one nucleus, reaches the surface at the nephridiopore posteriorly to the velum. The middle canal



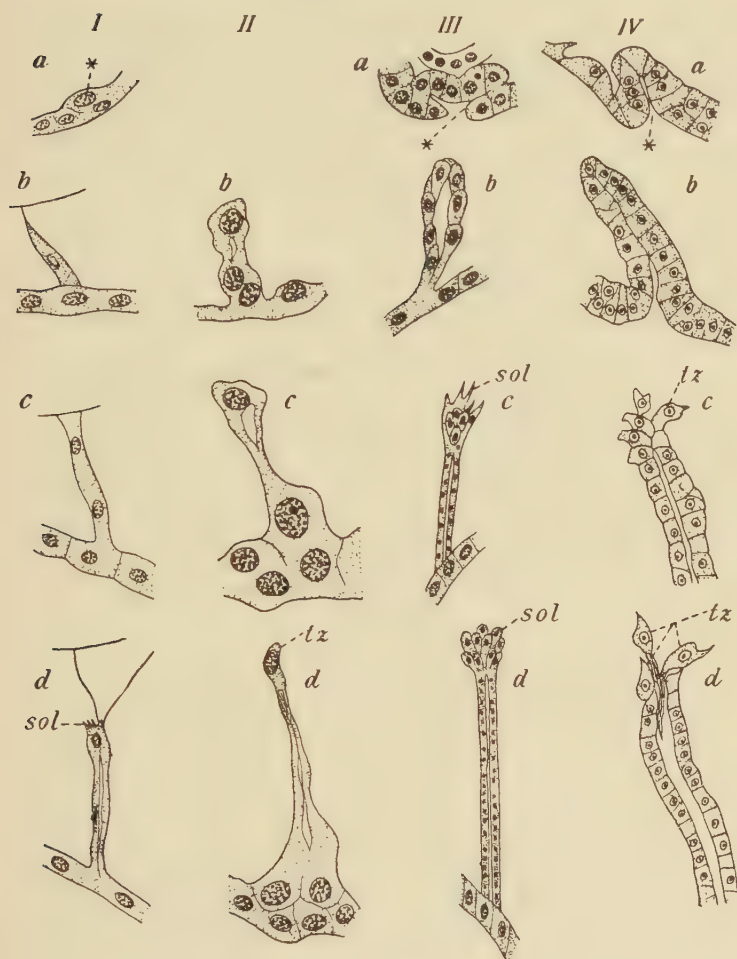
TEXT-FIG. 88.

Larval protonephridium of Basommatophora (Meisenheimer, 1899).

*äuss. Ö.*, external pore; *ect*, ectoderm; *ev*, vacuole; *k*, large nucleus; *ng*, excretory lumen; *tx*, terminal cell with flame of cilia, *wf*.

region contains a very large nucleus distally and a smaller nucleus proximally. A fourth nucleus belongs to the innermost cell closing the internal end. This is a large flame-cell bearing a bunch of long cilia which beat in the terminal chamber of the lumen. A few excretory granules may occur in the flame-cell, but are found chiefly in the cells of the canal. The terminal chamber has a very thin wall and serves no doubt for the passage of water which washes out the contents of the lumen (Willem, 1910).

In the Pulmonata Stylommatophora the structure of the larval protonephridia is somewhat different (Meisenheimer in *Limax*, *Arion*, *Helix*, *Succinea*). Here the canal has a multicellular wall with intercellular lumen. Its blind internal



TEXT-FIG. 89.

Development of larval protonephridia (from Meisenheimer, 1899).

I, *Polygordius* (Shearer, 1907); II, *Dreissensia* (Meisenheimer, 1900); III, *Phoronis* (Shearer, 1906); IV, *Limax* (Meisenheimer, 1898). *a*, *b*, *c*, *d*, consecutive stages; \* place of first origin; *sol*, solenocytes; *tz*, ciliated end-cells.

end is provided with two or more flame-cells (Text-fig. 89). The cell-body is set at the end of a thin-walled tube enclosing

the 'flame', and gives off irregular cytoplasmic processes projecting in the surrounding haemocoelic space. Such organs are remarkably like the solenocyte-bearing protonephridia of Polychaeta, or the larval protonephridia of Echiurus or Phoronis, differing from these chiefly in that the 'flame' is formed of several cilia instead of the single cilium characteristic of the typical solenocyte.

According to Meisenheimer (1900) the protonephridia of the larva of the Lamellibranch *Dreissensia* resemble those of Stylommatophora, but have only a single flame-cell at the inner end.

According to the careful studies of Meisenheimer, illustrated by convincing figures (Text-fig. 89), the protonephridia arise from the larval ectoderm, and certainly have nothing to do with the coelomic rudiment. In *Dreissensia* a proliferation inwards yields a small group of cells which acquire an intracellular lumen. The innermost cell becomes the terminal flame-cell, the more distal cells multiply to form the canal.<sup>1</sup>

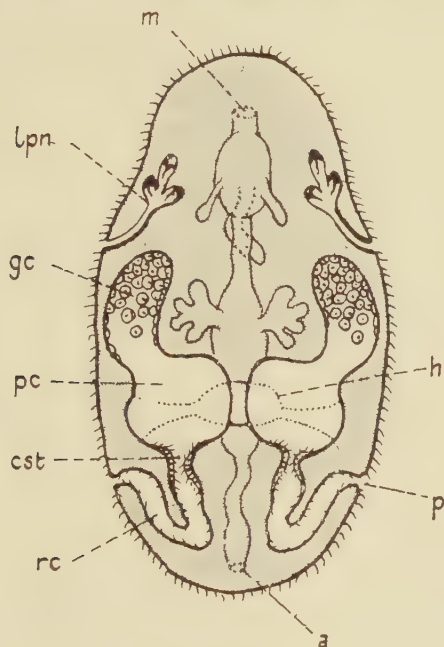
### General summary for Mollusca.

One may sum up concerning the Mollusca by saying that no adult Mollusc is known to possess nephridia, but that a pair of protonephridia opening posteriorly to the prototroch or velum may occur in the trochophore-veliger stages in Prosobranchs, Pulmonates, and Lamellibranchs. These larval kidneys may have a canal with intracellular or intercellular lumen. The blind internal end projecting into the haemocoelic space is

<sup>1</sup> Neither Stauffacher's (1897) description of the single protonephridium, occurring on the left side of the larva of *Cyclas* (*Sphaerium*), which is said to open internally (not confirmed by Willem, 1910), nor his conclusion that both ecto- and mesoblast contribute to its formation, can be accepted without confirmation.

Wierzejski's (1905) contention that in *Physa* the nephroblasts which give rise to the larval protonephridia are derived from the coelomesoblast, is so opposed to the results of other observers in Mollusca and to what has been clearly demonstrated in Annelida, that it could not be accepted without very definite evidence. No such evidence is given in his paper. The nephroblasts are not identified till there are more than 100 cells in the embryo, and their real origin remains unobserved in *Physa*.

provided with one or more flame-cells often closely resembling typical solenocytes, but with a flame of many cilia. The whole organ, both canal and flame-cells, develops from the larval



TEXT-FIG. 90.

Diagram of a primitive Mollusc, dorsal view. Each coelomic sac has a genital, *gc*, and pericardial, *pc*, chamber, and a coelomoduct with coelomostome, *cst*, and renal chamber *rc*. *a*, anus (ventral); *h*, heart; *lpn*, (larval) protonephridium; *m*, mouth (ventral); *p*, urinogenital pore.

ectoderm. These protonephridia disappear in later stages being functionally replaced by the adult kidneys of coelomic origin.

The coelom develops in paired coelomesoblastic masses; the right and left cavities may subsequently combine. Each coelomic sac tends to become subdivided into an anterior genital and a posterior perivisceral or pericardial chamber. From the posterior region of the latter chambers grow out a pair of coelomoducts which, having joined ectodermal ingrowths open

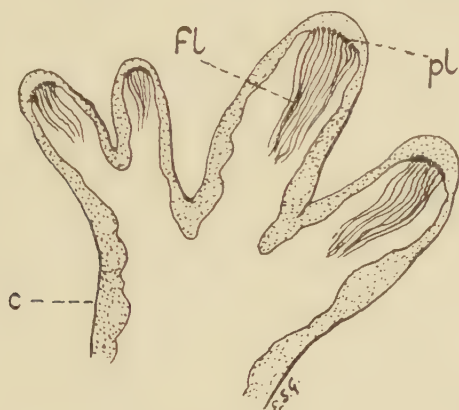
to the exterior and primitively serve as genital ducts (Text-fig. 90). The coelomostomes persist as the 'reno-pericardial' funnels. The epithelium lining the canal of the coelomoduct becomes excretory, and this region usually enlarges greatly to form the adult kidney, without in primitive forms losing its original genital function. But in Gastropods the genital function (and gonad) is lost on the left side, and in the more specialized forms the renal function (and kidney) may be lost on the right. In the higher Lamellibranchs the coelomoducts may become more or less completely subdivided into renal and genital ducts. Where, as in Polyplacophora and Cephalopoda, there are two pairs of coelomoducts (one genital and the other renal) their occurrence is probably due not to inheritance from a segmented ancestor but to the subdivision or the secondary duplication of the original pair.

The view adopted in 1895 (Goodrich, 1895) concerning the nature of the excretory and genital ducts of the Mollusca is here maintained. It is that the ancestral Mollusc had, in addition to nephridia, a pair of coelomic cavities (which became specialized into gonadal and pericardial chambers) and a corresponding pair of coelomoducts (Text-fig. 90). At first these latter served merely as genital ducts, but soon acquired an excretory function as well. The coelomostomes are probably represented throughout the Class by the renopericardial funnels, while the more distal part of the ducts has become enlarged into renal chambers. Meanwhile the nephridia, which never passed beyond the proto-nephridial stage, became reduced and completely lost in the adult, but persisted in several groups as larval excretory organs. They appear early, and develop from ectomesodermal or ectodermal cells, having nothing to do with coelomesoblast or adult kidneys. The few contradictory statements on their origin are shown to be based on insufficient evidence. The differences described in the development of the coelomesoblast are interpreted as due to secondary specializations.

When, as in Polyplacophora, Lamellibranchia, and Cephalopoda, there are special genital ducts and excretory ducts, this seems to be due to the splitting from coelomostome outwards of the original coelomoduct into separate passages to the exterior.

### Phylum Acanthocephala.

First noticed by Bojanus in 1821 in *Echinorhynchus gigas* the nephridia of the Acanthocephala are of considerable interest. Their true structure and function was first made out by Kaiser (1892). They have since been described by Schepotieff (1908), Kostylew (1918), Kilian (1932), and A. Meyer (1931, 1932-3).



TEXT-FIG. 91.

Diagrammatic optical section of blind ends of protonephridium of *Echinorhynchus gigas* (from a preparation kindly lent by Prof. A. C. Hardy). *c*, canal; *fl*, flame of cilia; *pl*, basal plate.

Although said to be absent in some, one pair of nephridia is now known to occur in many genera, attached to the dorsal surface of the genital ducts. They are of the protonephridial type; that is to say their inner extremities, projecting freely anteriorly into the body-cavity, end blindly and are provided with numerous hollow club- or finger-shaped processes inside which are 'flames' of cilia (Text-fig. 91).

In *Echinorhynchus* and several other genera the protonephridial canal ends in a bunch of arborescent processes bearing the flames at their tips (about 300 in the male, and as many as 600 in the female [Kaiser]; about 700 in the female *Hamanniella* [Kilian]). No nuclei are present on the flame-bearing clubs, and only three nuclei occur in the syncytial wall

at the base of the branches. The ciliated right and left canals join to a median expanded chamber which narrows again and opens in the ♀ into the base of the median oviduct before this enters the uterus, or into the median vas deferens in the ♂. Excretory products gathered in the nephridial chamber thus pass out through the vagina or penis, the openings of which function as urinogenital pores.

In *Oligacanthorhynchus* and *Pachyneutis* the inner end of the protonephridium is of somewhat different structure (A. Meyer). Here the canal expands into a rounded chamber, with three nuclei in its inner wall, and some 700 club-shaped processes containing flames of cilia radiating from its free surface.

From the above brief description it will be understood that the excretory organs of *Acanthocephala* differ considerably from the usual type of protonephridium. In the presence of 'flames' composed of many cilia they resemble rather the end-organs of the *Platyhelminia* than the solenocytes of the true *Coelomata*. Nor do the flame-bearing processes appear to be differentiated into well-defined rigid tubes as in the typical solenocyte. On the other hand, the presence of many 'flames' associated with each nucleus is foreshadowed in some *Platyhelminia*, and also occurs in certain annelids (see *Archianne-lids*).

What is the nature of the body-cavity into which they freely project is still doubtful. It does not appear to be a true coelom, since it is said to have no continuous epithelial lining and does not give rise to the genital products (although in the ripe ♀ the ova break through into the body-cavity owing to the disintegration of the wall of the ovisac). According to Kaiser the body-cavity arises from irregular spaces in the central mesodermal mass of the embryo.

The coelom seems to be represented by the paired genital sacs ('testes' and 'ovaries'); while the uterus bell (*Uterus-glocke*) and oviducts may be the highly specialized coelomoducts in the female. But the development of these organs is not yet sufficiently known to determine their homology in detail.

The combination of the nephridial and genital ducts to open

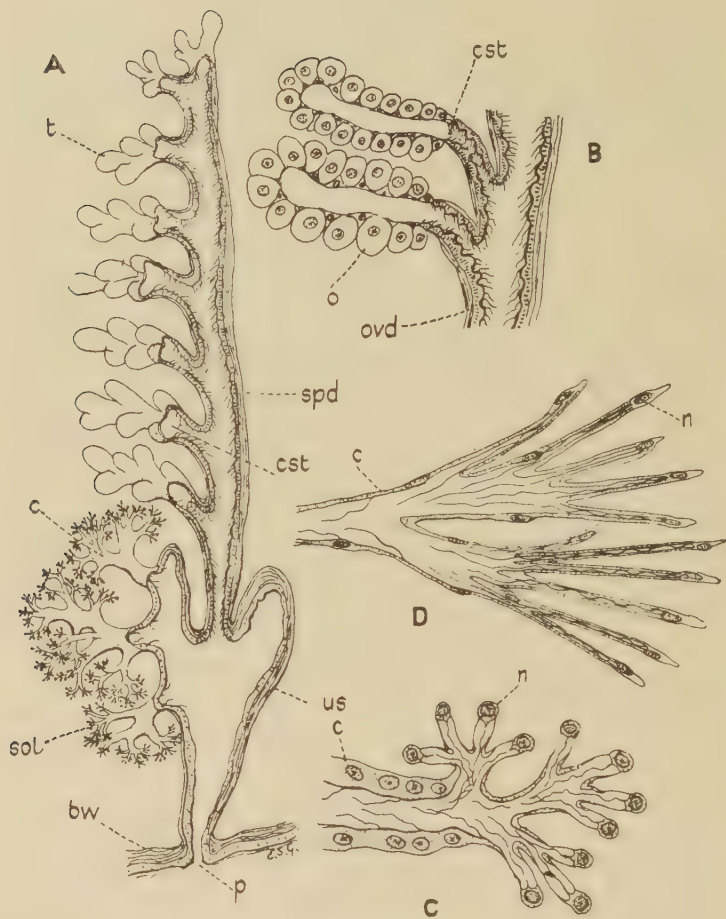
by a median canal and single urinogenital pore posteriorly gives rise to a nephromixial complex peculiar to the Acanthocephala. It may have been brought about by the carrying inwards of originally superficial paired excretory and genital pores by a median posterior ectodermal invagination.

### Phylum Priapulida.

It was Schauinsland (1886) who first made the interesting discovery of solenocyte-like cells in the Priapulida. The general anatomy of this group is now fairly well known but its systematic position is still very uncertain. The two known genera, *Priapul* and *Halicryptus*, differ little in structure, and the morphology of their excretory and genital organs is difficult to interpret (Apel, 1885; Horst, 1882; Schauinsland, 1886; Mottschanoff, 1908).

Enclosed by the muscular body-wall is an extensive continuous body-cavity said to be lined by a definite epithelium; but this statement requires confirmation. Hanging by longitudinal folds in this cavity, which is probably of a coelomic nature although the genital products appear not to be shed into it, are the paired urinogenital organs. They extend from the posterior end to about half-way up the body. In both sexes, on each side of the anus, is a urinogenital pore leading into an elongated sac—the urinogenital sinus—with a muscular wall and inner lining of columnar epithelium (Text-fig. 92A). Opening into the anterior region of the sinus is the genital pore at the end of a papilla. It leads into the longitudinal genital duct which ends blindly in front, but gives off along its course many blind lateral branches. The wall of the genital duct has a muscular coat and is lined by a ciliated epithelium differing considerably and sharply from that of the sinus. In the male the germinal epithelium lines the coecal extremities of the branches forming grape-like testes. At the base of each branch the inner epithelium forms a strongly ciliated funnel leading into the duct. The sperm is carried out at maturity by these funnels and duct into the sinus, and finally to the exterior by the urinogenital pore (Text-fig. 92A).

The female organs are built on the same plan as those of the



TEXT-FIG. 92.

*Priapululus caudatus*. A, Diagrammatic view of the urino-genital organs of a male, with urino-genital sinus, *us*, and spermiduct, *spd*, in section. B, Section of portion of oviduct, *ovd*, and ovarian sacs showing two coelomostomes, *cst*; *o*, ovum. C, Branch of protonephridial canal, *c*, with solenocytes, *sol*, possessed of apical nuclei, *n*. D, Branch with elongated solenocytes projecting beyond nuclei. *bw*, body-wall; *p*, urino-genital pore; *t*, testicular sac.

male, but the blind side branches of the longitudinal oviduct expand into closely packed ovigerous hollow lamellae the walls of which are formed by the germinal epithelium (Text-fig. 92 B). The ripening ova come to bulge on their outer surface and seem later to return to the lumen, as maintained by Schauinsland (1887). Thence they are carried by the ciliated funnels into the oviduct and urinogenital sinus.

These funnels and ducts in both sexes appear to be of the nature of coelomoducts. There are as many funnels as there are gonadal diverticula, and the funnels and duct on each side may be interpreted as either a number of coelomostomes whose canals have joined and combined to form a single duct opening into the sinus; or, more probably, as a single coelomoduct whose coelomostome has become subdivided into many funnels.<sup>1</sup>

The excretory organs are protonephridia (Text-fig. 92 c, d) provided with a multitude of solenocytes projecting freely into the body-cavity near the base of the genital ducts. What appear to be outgrowths of the anterior wall of the sinus itself, lead to thinner-walled canals whose short blind tufted branches bear the solenocytes. The excretory products pass into the sinus, and so to the exterior by the urinogenital pore. The solenocytes are of fairly typical structure, with apical cell-body and nucleus, a single long flagellum, and well-defined thin-walled tube.<sup>2</sup>

Not until the development of these organs becomes known shall we be able to give a satisfactory explanation of their general morphology.<sup>3</sup> But it may even now be pointed out that

<sup>1</sup> The description given above of the urinogenital organs is founded on *Priapulus*, and differs considerably from that of previous authors, especially with regard to the sinus. In preparing this account I have had the advantage of studying preparations and drawings kindly lent to me by Professor A. C. Hardy, and of discussing the subject with him.

<sup>2</sup> Hardy discovered, and I can confirm his observation, that some of the terminal branches of the protonephridial canals bear very slender twigs ending in elongated solenocytes differing considerably from the more ordinary ones (cf. Text-fig. 92 c and d). In these the long oval nucleus is situated some little distance from the apex.

<sup>3</sup> Hammarsten (1915) and Eggers (1925) have given short accounts of some larval stages of *Halicryptus*. In the earliest Hammarsten found the protonephridia were alone present, later stages seem to differ little from the adult. Both authors describe the outgrowth of successive

they constitute almost certainly some kind of protonephromixium. Either the protonephridium and the genital coelomoduct originally opened independently to the exterior, and owing to the invagination of a common ectodermal sinus have acquired a single urinogenital pore; or the sinus is an expanded chamber of the nephridial canal into which the coelomoduct has come to open—as in *Phyllodocids*.

The whole urinogenital complex somewhat resembles that of the *Acanthocephala*, sometimes considered to be related to the *Priapulida*; but the solenocytes differ considerably in the two groups, those of the *Acanthocephala* having no apical nucleus and a 'flame' of cilia instead of a single flagellum.

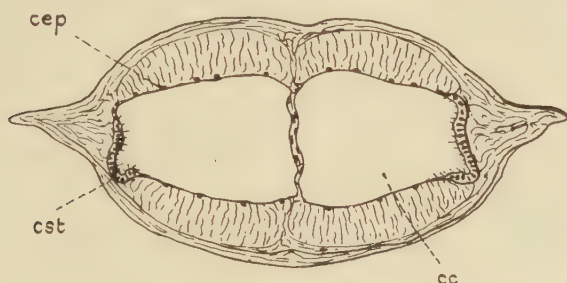
### Phylum Chaetognatha.

The structure of the *Chaetognatha* is very specialized, and there is no evidence of the presence of nephridia. Nevertheless, in the possession of definite coelomic cavities, and as regards their male genital ducts, they seem to conform to the usual coelomate plan.

They are hermaphrodite. The body contains a pair of anterior coelomic chambers in the trunk region and a pair of posterior coelomic chambers in the caudal region, divided by a longitudinal median mesentery enclosing the gut in the trunk. Immediately behind the ventral anus is a transverse septum dividing the anterior from the posterior chambers. The coelom is lined by a sparsely ciliated epithelium. The primordial germ-cell appears early in cleavage, divides twice, the four resultant cells coming to lie right and left on the anterior and posterior surfaces of the transverse septum. The anterior cells give rise to the two ovaries, the posterior to the two testes (Doncaster, 1902). Each germ-cell becomes covered by overgrowing coelomic epithelium and forms a band of germinal tissue bulging into the coelom and attached to the lateral wall by the enclosing fold of epithelium. From the testes developing spermatogonia fall into the coelomic cavities of the caudal region. The sperma-

solenocyte-bearing tufts from the gonadal duct itself. This observation would be difficult to reconcile with the adult structure, and cannot be accepted without more convincing evidence and detailed figures.

tozoa are carried to the exterior by a pair of sperm-ducts. Each duct has an internal ciliated funnel-shaped opening about half-way down the caudal coelom, and a narrow lateral ciliated canal leading posteriorly to an enlarged sperm-vesicle. This vesicle at maturity becomes swollen with sperm, and projects laterally from the tail with the genital pore at its end. Doncaster, on



TEXT-FIG. 93.

*Spadella cephaloptera*. Transverse section of caudal region.

cc, caudal coelom; cep, coelomic epithelium; cst, coelomostome (sperm-funnel).

quite inadequate evidence, concluded that the sperm-duct was developed as an ingrowth of the ectoderm; but there can be little doubt that it is a coelomoduct derived from the wall of the caudal coelom. In *Spadella*, for instance (Text-fig. 93), I find the funnel to be large and spreading with the margin of the lip continuous with the thinner lining of the coelom. It has all the appearance of a typical coelomostome.

The female ducts are more difficult to interpret, though, being derived from the coelomesoblast, they may possibly be highly modified coelomoducts without permanent internal openings.<sup>1</sup>

<sup>1</sup> The anterior pair of embryonic germ-cells mentioned above multiply forming two longitudinal bands of ovarian tissue attached to the outer wall of the right and left coelomic trunk cavities by the covering epithelium. The structure and function of the ducts have been elucidated recently chiefly by Stevens (1910), whose observations have been extended and confirmed by Bordas (1920) and Burfield (1927). Running along the outer side of the ovary is a flattened canal, the oviduct. The band of germinal

### Phylum Sipunculida.

The Sipunculids have a pair of large so-called 'nephridia' (in some species only one, either right or left is present) (Hérubel, 1907; Harms, 1921). From the ventral pore a short canal, piercing the body-wall and provided with a sphincter muscle, opens into the saccular excretory main chamber lined with ciliated excretory cells. This chamber projects into the coelom, and opens into it by a wide funnel of ciliated epithelium close to the external duct. The lips of the funnel are continuous with the coelomic epithelium, the outer one spreading on the body-wall, the inner and shorter one projecting freely. These organs, which function as both excretory and genital ducts, have in the adult the appearance of being nephromixia, and resemble

epithelium is set along the middle region of the inner wall of this canal, the outer edges of which are bent inwards so as partially to enclose the ovary. Both ovary and canal are enclosed in the same covering layer of coelomic epithelium. The oviduct ends blindly near the anterior tip of the ovary, but opens to the exterior posteriorly on a lateral papilla. Running inside the oviduct along its whole length is another tube, tapering to a blind end in front but dilating posteriorly before it narrows again to open posteriorly by a pore at or close to the oviducal pore. In *Spadella* I find that the two tubes open by a common thick-walled duct, probably an invagination of the ectoderm.

The wall of the oviduct is of columnar epithelium, that of the inner tube of a syncytium with many nuclei. This inner tube, wrongly called 'sperm duct' by Stevens and Burfield, functions as a receptaculum seminis (spermatheca), and receives ripe sperm at copulation from the vesicula seminalis of another individual.

At intervals along the oviduct ripe ova approach its wall, and each becomes fertilized by a spermatozoon passing through a connecting bridge composed of two perforated accessory cells (derived from the oviducal wall) from receptaculum to ovum. The inner accessory cell sinks into the ovum through a micropyle in the now thick vitelline membrane. The micropyle closes behind the spermatozoon, and the fertilized egg makes its way through the wall of the oviduct and down this duct until it reaches the exterior. The hole in the oviducal wall closes up.

The development of the oviduct and receptaculum is not completely known, but the layers from which they are formed seem to be derived from folds and proliferations of the coelomic wall along the outer side of the ovary. Probably these organs are two pairs of coelomic sacs each with a pair of coelomoducts. But more information is required before the morphology of the Chaetognatha can be explained.

the mixonephridia of many Polychaeta. We may be sure they are not mere metanephridia in the sense here defined.

There are no special larval protonephridia, but the definitive organs appear early in *Sipunculus nudus* according to Hatschek (1884). In the young spherical larva he describes on either side a single large cell loaded with yellow granules and situated in the outer layer of the developing coelomic sac. The exact origin of this nephridioblast is not recorded. Later it bulges into the coelom covered by epithelium. The yellow cell then divides, forming a mass of three colourless cells and one yellow cell against the ectoderm. The colourless cells multiply and grow into a U-shaped loop with a lumen which comes to open into the coelom by a ciliated funnel derived from the peritoneum. The yellow cell divides to form the external duct and pore. The sac-like shape of the adult organ is only acquired at metamorphosis.

The later account given by Gerould (1906) is unfortunately less complete.<sup>1</sup>

Thus, although the evidence is consistent with my view (1895) that the organ is of double origin (formed of a nephridium and a coelomostome), the proof that Hatschek's yellow cell is not derived from coelomesoblast is still missing.

### Phylum Phoronida.

It is now well known that while the *Actinotrocha* larva of *Phoronis* is provided with a pair of protonephridia, the adult has paired organs with large coelomic funnels serving as genital ducts. Caldwell (1882) was the first to describe the larval nephridia correctly as having blind internal ends with peculiar excretory cells, similar to those described by Hatschek in the

<sup>1</sup> Gerould found it difficult to trace the origin of the excretory organs in *Phascolosoma*, and observed them only after metamorphosis as a pair of ingrowths probably from the ectoderm. Each is then a retroperitoneal mass of cells with a central lumen. 'The nephrostome is soon established as a channel which passes through the anterior side of the base of the rudiment of the nephridium, the cavity of which it connects with the coelom. The walls of this passage, which later become ciliated, are formed from mesoderm. A narrow tubular nephridiopore becomes visible at about the time that the nephrostome is formed', p. 119. (Gerould, 1906.)

larva of *Echiurus*. Twenty years later (Goodrich, 1903) it was shown that the thin-walled expanded end of the protonephridium which projects into the haemocoel (?) anterior to the transverse septum is beset with numerous solenocytes (Text-fig. 64 A). The nucleated cell-body of the solenocyte is situated near the free tip of the rather wide tube down which a single flagellum passes into the lumen of the canal.<sup>1</sup> The relatively thick-walled canal of excretory ciliated epithelium leads to a ventral pore posterior to the attachment of the septum. Cowles (1905) independently reached the same conclusions, which have also been confirmed by Selys-Longchamps (1904 and 1907), Shearer (1906), and Schepotieff (1906).

In a later description of the protonephridium of *Actinotrocha branchiata* a further observation of considerable interest was brought to light (Goodrich, 1909), as explained in the quotation given below<sup>2</sup> and shown in Text-fig. 64 A. It relates to the existence of delicate long cilia springing from the outer surface of the protonephridium among the solenocytes, and thus situated in the pre-septal space generally believed to be haemocoelic. They closely resemble similar cilia on the protonephridia of certain Phyllodocids (Goodrich, 1900; Fage, 1906; see Text-fig. 21). But in these Polychaetes the cilia are,

<sup>1</sup> Irregular tapering processes extend freely from the apex of the cell-body, as in many other forms such as *Polychaeta*, (Text-fig. 34). Another detail concerns the nucleus of the solenocyte. In some species it is of crescentic shape, being somewhat curved round the tube. Thus 'the solenocytes often present the appearance of possessing 2 or 3 nuclei' (Goodrich, 1903, p. 114). Cowles (1905) figures two nuclei, but I am still of the opinion that there is only one.

<sup>2</sup> In this form (*Actinotrocha branchiata*) it [the nephridium] is a large organ with a branched internal end lying in the pre-septal haemocoel . . . multitudes of solenocytes project from the wall of the nephridial canal. . . . Now it is well known that an accumulation of blood-corpuscles is generally found in the neighbourhood of the nephridium in these larvae, and the interesting new point I have to bring forward, and already mentioned above, is this—that very long stiff cilia are set among the solenocytes, attached by their base to the wall of the nephridium between the solenocyte tubes. Although I did not observe these cilia move very actively in the larva compressed under a cover-slip, yet I have little doubt that they agitate the blood-fluid, and so lead to the gathering of the corpuscles.

of course, in the coelom; the mere presence in the larva of *Phoronis* of cilia in what is generally held to be a true blood-space is most remarkable, and indeed unique, so far as I know. It suggests that, after all, this pre-septal space in *Phoronis* may be coelomic, and comparable to the so-called Polian ring-canal (with its tentacular branches and Polian sacs) found in *Sipunculida*; for the cells of the internal lining of this canal system may also be ciliated.

The development of the protonephridia of the *Actinotrocha* larva is important because it is one of the few cases in which it has been definitely established that the whole organ is derived from the ectoderm.

As Ikeda (1901) first showed, they arise from a median ventral ectodermal pit close to the larval anus. This observation has been confirmed by Cowles (1905), Selys-Longchamps (1904, 1906), and Shearer (1906), who has given the most detailed account of the development.

The pit is formed as a hollow ingrowth of the ectoderm in the quite young larva; it soon bifurcates, its two branches being the rudiments of the two protonephridia. The pit and its pore becoming subdivided, the two rudiments come to open separately. Each has a lumen enclosed by many cells, and those towards the inner free end are drawn out to form the solenocytes. Thus, in *Actinotrocha*, both canal and solenocytes are derived from the same ectodermal rudiment, and have nothing to do with the coelom but grow in origin. Nor are the solenocytes derived from mesoblastic mesenchymatous cells as suggested by Ikeda. The nephridiopores, at first near the anus, remain anteriorly near the transverse septum as the anus is carried away at the posterior end of the growing larval trunk.

The adult *Phoronis* likewise has a pair of organs, generally called 'nephridia', but of a very different type (Caldwell, Benham, Cori, Cowles, Selys-Longchamps). Each is composed of a retroperitoneal ciliated canal running in the body-wall, and opening on the one hand to the exterior by a pore at the side of the anal papilla, and on the other hand, into the post-septal coelom of the trunk by one or two wide ciliated funnels. This post-septal coelom; into which the genital products are

shed, is partially subdivided by a median ventral mesentery and by two lateral mesenteries (incomplete posteriorly) into two lateral chambers and one dorsal rectal chamber. In those species with one funnel it opens into the lateral chamber; in the others the smaller funnel opens into the lateral and the larger into the anal chamber.<sup>1</sup> *Phoronis* is hermaphrodite, and the chief function of these organs is to carry the ripe genital products to the exterior, but they also appear to expel waste substances and the epithelium of the canal shows some signs of being excretory, unlike that of the funnel.

In 1895 and 1903 I suggested that the genital ducts of *Phoronis* are not mere nephridia but compound organs made up of a coelomostome grafted on to a nephridial canal. Caldwell (1882) had maintained that at metamorphosis the inner end and solenocytes of the larval kidney were cast off into the haemocoel, but that its canal persisted as that of the adult organ. Ever since most authors have adopted his interpretation. Selys-Longchamps (1904) confirmed his account of the fate of the solenocytes, and maintained that the canal persisted and the funnel must be added from the coelomic epithelium. The continuity of its lip with this epithelium, and the histological structure of the funnel support this view that it is indeed a coelomostome; but that the adult canal is of separate origin and derived from the larval protonephridium seems never to have been actually proved. As Cori remarks (1939) it is still an open question.

<sup>1</sup> In such forms as *Phoronis psammophila* and *Phoronis architecta* with one funnel there is below the transverse septum an opening through the lateral septum, and the lip of the funnel spreads over its free edge and on to the posterior surface of the septum; but in *Phoronis australis* and *Phoronis hippocrepi* the two funnels appear to have been formed by the further spreading of the funnel epithelium so as to enclose the passage, thus giving rise to a bifurcating tube, each branch leading to a funnel on either side of the mesentery, as shown by Selys-Longchamps (1906). This author has rightly pointed out an unaccountable but inexcusable mistake made by me (Goodrich, 1895, 1903) in stating that one funnel opens into the pre-septal and the other into the post-septal coelom, instead of into the lateral and the anal chambers of the post-septal coelom

### Phylum Brachiopoda.

No very definite advance has been made in our knowledge of the so-called 'nephridia' of Brachiopods since 1895, when we concluded that these organs which function both as excretory and genital ducts may be of the nature of nephromixia. There is usually a pair, but Morse found two pairs in *Hemithyris*. Each consists of a deeply pigmented excretory canal opening by a pore to the exterior, and by a wide colourless funnel into the coelom.

Blochmann (1892-1900) has continued his description of them in various genera, and Morse (1902) has added interesting observations calling particular attention to the deep grooves and ridges on the ciliated surface of the widely open funnels. In this they resemble the coelomostomes of many Polychaeta. Schaeffer (1926) has recently given a good description of the ducts in *Lingula*, showing that the lip of the funnel is continuous with the coelomic epithelium, and that the histological structure of its epithelium changes suddenly as it reaches the lining of the canal composed of cells loaded with excretory granules. She concludes that the organs are probably nephromixia; but the accounts of their development in the larva of *Lingula* by Yatsu (1902) and of *Cistella* (*Argiope*) by Plenk (1915) are too incomplete to enable us to decide the question for certain.

The Hemichordata, Echinodermata, and Tunicata are a group of related forms in which the nephridia seem to have been entirely lost, the function of excretion having been assumed by coelomoducts or some other organs. Except in the Tunicata, paired segmental coelomesoblastic sacs persist with coelomoducts. The genital ducts are probably always of coelomoduct nature. Since 1895 nothing of great importance seems to have been discovered about the general morphology of these organs in Echinoderms and Tunicates.

### Phylum Hemichordata.

The Class Hemichordata includes the Enteropneusta (*Balanoglossus* and its relatives) and the Pterobranchia (Ce-

phalodiscus and Rhabdopleura). It is related on the one hand to the Echinodermata, and on the other to the Vertebrata. Van der Horst (1939) has recently given a good account of the whole group.

They all have three consecutive pairs of anterior coelomic cavities (proboscis, collar, and trunk coeloms), and separate genital sacs in the trunk region (Text-fig. 94). The proboscis cavities and the collar cavities communicate with the exterior by 'pores'.<sup>1</sup> The trunk cavities are closed, but Willey's 'truncal canals' in *Spengel* (1899) may represent a third pair of coelomoducts.

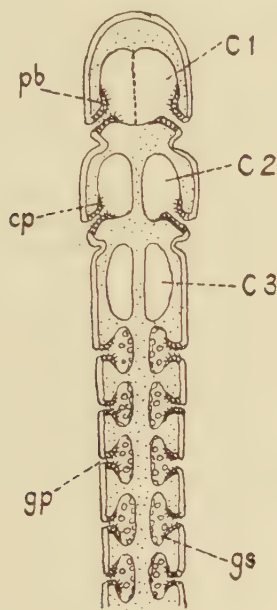
Various authors have compared these pores to 'nephridia';

<sup>1</sup> Each 'pore' is in the form of a tubular canal of thick ciliated epithelium continuous distally with the epidermis, and opening internally by a funnel the lip of which is continuous with the coelomic epithelium. Although several authors believe the canal to be of ectodermal origin, its development is not thoroughly well known. It is best described by Willey (1899) in *Enteropneusta* as formed by the combination of an outgrowth from the coelomic wall with an ingrowth of the ectoderm. From the former he derives the funnel and part of the canal, from the latter the terminal exit canal with the vesicle or expansion often here developed. This account agrees with the observations of Dawydoff (1907) on the regeneration of this organ in *Ptychodera minuta*. Here the inner region, including the funnel and the greater part of the canal, develops from a thickened patch of the coelomic epithelium, while the more distal part is formed from an invagination of the epidermis (such as so generally occurs when a tubular organ opens on the surface).

In the *Enteropneusta* both the anterior coelomic cavities taper posteriorly to form canals leading to paired dorsal pores at the base of the proboscis in such genera as *Harrimania* and *Stereobalanus*, but in many (*Balanoglossus*, *Ptychodera*, and others) only the canal and pore on the left side are fully developed, and the pore may become median. On the right side the coelomic diverticulum may be solid or fail to reach the epidermal invagination, a vestige of which may however be present (Willey, 1899).

Concerning the larval development we know from the early work of Bateson, Morgan, and Spengel, that the proboscis pores of the *Tornaria* larva are formed from outgrowths of the anterior coelomic cavities which meet the ectoderm. More recently Spengel, 1893, Stiasny, 1914, and Heider, 1909, have produced further evidence; but the exact limit between the two layers in the completed structure is obscure. Undoubtedly they are homologous with the similar 'water pores' of Echinoderm larvae.

without, however, distinguishing between nephridia and coelomoducts. That they are not true nephridia can hardly be doubted; but their structure and development support the



TEXT-FIG. 94.

Diagram of *Balanoglossus* showing paired series of coelomic somites each with a coelomoduct.  $c^1$ , proboscis,  $c^2$ , collar, and  $c^3$ , trunk coelom;  $cp$ , collar pore;  $gp$ , genital pore;  $gs$ , genital coelom;  $pb$ , proboscis pore (Goodrich, 1895).

view put forward by me (Goodrich, 1895) that they are the coelomoducts of the corresponding segments. No good evidence of the presence of nephridia has yet been found. The description of solenocytes in *Cephalodiscus* by Schepotieff (1907) has not been confirmed, and seems to have been founded on erroneous observation (Andersson, 1907; Ridewood; Goodrich).

Proboscis and collar pores seem to have little if any connexion with excretion in adult Hemichordates. Spengel suggested that

their function is to regulate the turgity of the anterior regions of the body, and this seems to be the explanation of the retention of the coelomoducts in these anterior but now sterile segments.

The Pterobranchia have a pair of pear-shaped genital sacs projecting into, but closed off from, the coelom of the trunk. From the inner lining epithelium of each sac are developed the genital cells, which escape by a short duct to the exterior. Similar sacs occur in the trunk of the Enteropneusta; from each grows out a duct to open at maturity to the exterior.

These genital follicles have been considered by me (Goodrich, 1895) as posterior coelomic somites opening by coelomoducts fulfilling their original function. In the Enteropneusta some kind of secondary multiplication seems to have taken place, either by subdivision or by repetition leading to the modification of their presumed original segmental disposition (as in Nemertina). Willey (1899) agrees with my view that the genital sacs were primitively arranged metamerically.

We may conclude that the Hemichordata were originally provided with a series of paired segmental coelomic cavities, each with a coelomoduct opening to the exterior; that the first three pairs of cavities have been modified in adaptation to the mode of life of the adult, becoming large and sterile, but in the case of the first two retaining coelomoducts in the form of proboscis and collar 'pores'; that the coelomic cavities and coelomoducts of the trunk are represented by the genital follicles and their ducts. No nephridia have yet been found in either adult or larva.

### Phylum Echinodermata.

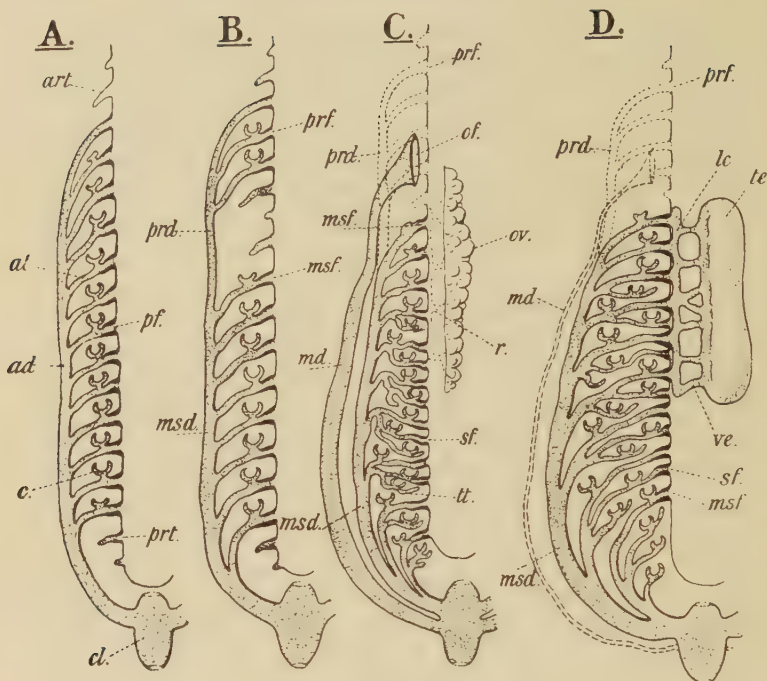
Although the adult Echinoderms are so modified in structure owing to the imposition of a secondary radial on the original bilateral symmetry, they are known from their development to be built on the same fundamental plan as the Hemichordata, with three successive pairs of coelomic sacs: the anterior pair corresponds to the proboscis coelom; the middle pair corresponds to the collar coelom; and the posterior pair to the first trunk coelom (Goodrich, 1895). From the first develops, as a rule

only on the left side, a coelomoduct which becomes the stone-canal. Of the second pair only the left is normally developed. It arises as an outgrowth of the left anterior coelom, and remains connected with the stone-canal. The gonads, perigonadial sac, and at least the proximal region of the genital ducts, are derived from the wall of the left posterior coelomic sac. The ducts may, therefore, represent the coelomoduct of the posterior segment.

### Phylum Vertebrata.

**General Morphology of the Excretory Tubules and Genital Ducts of the Craniata.**—Ever since the 70's of the last century the excretory tubules of the Craniata were compared to those of the Annelida (Gegenbaur, Semper, Balfour, and others), and when Lankester (1877) introduced the term nephridium for the excretory organ of the earthworm it was generally accepted that the kidney tubules of Craniata were homologous with the segmental nephridia, differing from these chiefly in that they opened to the exterior not separately by segmental pores but into longitudinal ducts passing back to the cloaca. This theory became so firmly established that it survives to the present day in spite of accumulating evidence against it. For it was pointed out (Goodrich, 1895) that two different organs had been confused under the same name: (1) the primarily excretory nephridia not derived from the coelomic wall, and (2) the primary genital ducts (genital funnels, or coelomoducts) derived from funnel-like outgrowths of the wall of the coelomic somites. It then became obvious that the segmental tubules of the Craniata are homologous not with the nephridia but with the coelomoducts of the Invertebrates, and the very foundation of the theory, as hitherto defined, was upset.

No attempt will be made to describe in detail in this paper the development of the craniate kidney which has already been done in many special works and summarized in many textbooks (including my own book on Vertebrates, 1930); but it may be stated that it is now generally accepted that the excretory tubules in Craniata develop directly or indirectly as



TEXT-FIG. 94 A.

Diagrams of the urinogenital system in Craniata. A, Hypothetical ancestral stage with continuous archinephros. B, Cyclostoma with pro- and mesonephros. C, Female adult gnathostome. D, Male adult Gnathostome. *ad*, archinephric duct; *art*, anterior vestigial tubule; *c*, Malpighian capsule; *cl*, cloaca; *lc*, longitudinal canal; *md*, Müllerian duct; *msd*, mesonephric duct; *msf*, mesonephric funnel; *of*, oviducal funnel; *ov*, ovary; *pf*, coelomostome; *or*, peritoneal funnel; *prd*, pronephric duct; *prf*, pronephric funnel; *pvt*, posterior vestigial tubule; *v*, vestigial vasa efferentia; *sf*, secondary funnel; *te*, testis; *tt*, tertiary tubule; *ve*, vas efferens. The vestigial oviduct on the embryonic pronephros are in dotted lines in c and d (Goodrich, 1909).

more or less funnel-shaped paired outgrowths from the wall of the coelomic somites. No doubt they originally were formed in every segment of the body, but they tend to disappear both in the head and tail regions (Text-fig. 94 B).<sup>1</sup>

<sup>1</sup> The theory that the 'water pores' of Echinodermata, the 'proboscis

Moreover, while it may be assumed that in the remote ancestor these segmental coelomoducts opened independently to the exterior, in all known Craniata their distal ends combine to form longitudinal ducts leading backwards into a cloaca or its derivative (Text-fig. 94A).<sup>1</sup>

The old theory of the homology of the vertebrate tubules must, therefore, be recast in conformity with modern knowledge (Goodrich, 1895, 1902, 1930),<sup>2</sup> and may be stated as follows: The segmental tubules developed from the wall of the coelomesodermal somites in Craniata are coelomoducts homologous with those of the Triploblastic Invertebrata in general. Their function was originally to act as genital ducts; but, accompanying the disappearance of the primitive excretory nephridia, they assumed the function of excretion.

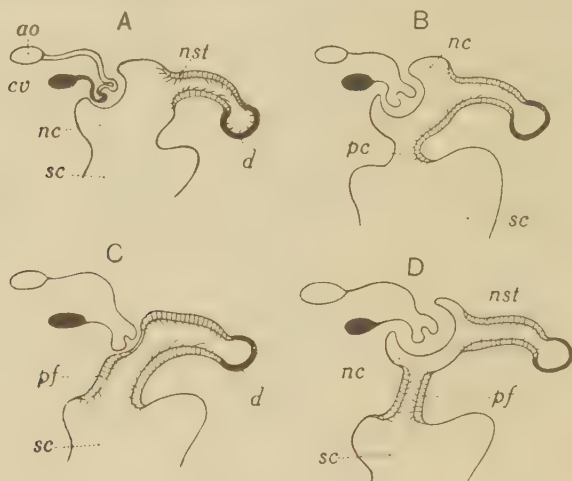
Before discussing the question further it is necessary to explain the relation of the tubules to the coelomesoblast and coelom in development. It may be stated quite briefly as follows, giving only the main results applicable to Craniata in general: From the embryonic mesoblast become differentiated from

pores' of Enteropneusta, the coelomesodermal portion of Hatschek's pit in Acrania, and ducts leading into the hypophysis of certain Craniata, are all homologous and represent the coelomoducts of the first pair of somites has been put forward (Goodrich, 1917).

<sup>1</sup> In Cyclostomata there are paired genital funnels opening into the cloaca anteriorly to the urinary pore. They probably represent a pair of coelomoducts not involved in the formation of the longitudinal excretory duct. The combination of genital coelomoducts to form longitudinal ducts occur also in Oligochaeta, and in Hirudinea.

<sup>2</sup> In a general account of the excretory organs of the vertebrata van der Broek (1938) puts forward the strange theory that the segmental tubules of Craniata are nephromixia! While accepting my conclusion that the peritoneal funnel is a coelomostome he claims that the remainder of the tubule and the longitudinal duct are of protonephridial origin!! Evidence for this theory seems to be entirely absent. It may be added that the author's knowledge of nephridia, coelomoducts, and nephromixia seems to be derived from the work of Felix (1904-5), to whom he appears to attribute the distinction between these various organs, and also the conclusion that the excretory tubules of Craniata are homologous with the genital coelomoducts of Invertebrata. This conclusion was first expressed by me in 1895, and has been repeated and extended by me in many works since.

before backwards a right and left series of coelomesodermal segments enclosing coelomic cavities. Each such lateral band retains its segmentation dorsally (somites), but loses it ventrally where a continuous lateral plate is formed by fusion, containing



TEXT-FIG. 94 B.

Diagrams of segmental excretory tubules (coelomoducts) of Vertebrates. A, Usual condition of pronephric tubule. B, Hypothetical intermediate condition. C, Supposed primitive condition. D, Complete tubule, pronephric or mesonephric. *ao*, dorsal aorta; *cv*, cardinal vein; *d*, longitudinal duct in transverse section; *nc*, nephrocoele; *nst*, nephrocoelostome; *pc*, communication between latter and splanchnocoel, *sc*. This passage corresponds to peritoneal funnel, *pf* (Goodrich, 1930).

a continuous 'general coelom' or splanchnocoel. Thus by further differentiation arise segmental dorsal epimeres (from which are formed the myotomes and their myocoels, and the sclerotomes), the ventral hypomeres which contribute to the unsegmented lateral plate (yielding visceral musculature), and connecting intermediate mesomeres which yield the segmental kidney tubules). At first myocoel, mesocoels, and splanchnocoel are continuous; but soon the myotomes and their myocoels are separated off from the more ventral mesomeres and their mesocoels. In those segments of the trunk in which tubules

are to develop the segmental mesomeres persist opening into the splanchnocoel; they generally enlarge somewhat and are known as nephrotomes and their coelomic cavities as nephrocoels (Bowman's capsules of adult). Their communication with the splanchnocoel may persist in the adult as ciliated peritoneal funnels.

This condition may be reached directly as described above, or secondarily when the mesomere develops more or less independently as an 'intermediate cell-mass' in which a nephrocoel appears. The cell-mass, of coelomesoblastic origin, may establish a connexion with the lateral plate, and the nephrocoel come to open secondarily into the splanchnocoel.

It is from the outer wall of the nephrotome that the tubule develops as a conical outgrowth into which penetrates the nephrocoel. These rudiments growing outwards and backwards from successive segments combine distally to form the longitudinal ducts which come to open posteriorly into the cloaca or its derivative.

Thus, while the whole tubule (and the ducts which may be derived from it) is ultimately developed from the segmental coelomesodermal mesomere, it may be distinguished into different parts of different functions and of different mode of development. Not all of these parts are necessarily found either in the embryo or in the adult. A complete fully developed Craniate tubule may be said to consist of (1) a ciliated peritoneal funnel opening from the splanchnocoel, and leading to (2) a thin-walled chamber (Bowman's capsule derived from the nephrotome and containing the nephrocoel) one side of which is pushed in by the vascular glomerulus to make up the adult functional Malpighian body; and lastly (3) the outgrowth from the capsule which becomes the 'glandular' tubule, and leads back to the longitudinal duct and so to the exterior.

Parts 1 and 2 are formed by the direct conversion of the middle region (mesomere) of the segmental coelomesodermal coelomic sac, while part 3 is derived from a new coelomoduct-like outgrowth of the nephrotome.

As the Craniate urinogenital system became more specialized it would seem that the tubules for the most part tended to

become purely excretory. These tubules tended also to become secondarily multiplied while restricted to fewer and fewer segments in the mid-region of the body in the adult. Yet some of the originally complete series of coelomoducts always contribute to the formation of the genital ducts. In Cyclostomata it is apparently a posterior pair which remains as genital ducts (so-called genital pores opening into the cloaca). In Gnathostomata the genital duct of the female (Müllerian duct) is formed from quite anterior coelomoducts which extend backwards; while in the male it is those of the mid-region which carry the sperm to the exterior; the coelomoducts involved thus lose the secondarily acquired excretory function and return in the adult to a purely genital function in the highest forms (Amniota).<sup>1</sup>

### Protonephridia of the Acrania.

Paired Protonephridia.—The conclusion, mentioned above, that the ancestors of the Vertebrata possessed nephridia

<sup>1</sup> Concerning the morphology of the Craniate tubule there is a point which remains undecided as to the exact homologue of the coelomostome. It is well known (see Semon, 1892; Goodrich, 1930) that the complete typical tubule is provided with two funnels: one leads from the general coelom into the nephrocoel (cavity of the Malpighian capsule), the other leads from the Malpighian capsule to the longitudinal duct (Text-fig. 94 B). They are the 'outer' and 'inner funnels' of Semon, named by me the 'peritoneal funnel' and 'nephrocoelostome' respectively. The question is which of these two funnels represents the primitive coelomostome? If it is the peritoneal funnel, then the nephrocoel of the capsule must be considered as an enlargement of the lumen of the coelomoduct; if it is the nephrocoelostome, as I am inclined to believe, then the nephrocoel is to be considered as a segmental dorsal chamber separated off from the general unsegmented coelom below, but retaining its communication by means of the narrow peritoneal funnel. A third possibility is that both funnels have been derived from the original coelomostome by some process of subdivision. It does not seem possible at present to decide which of these interpretations is the correct one (Goodrich, 1930, p. 718). The problem is of some interest, but is not of fundamental importance. For it must be remembered that no hard and fast line can be drawn between a coelomostome and the coelomic epithelium from which it is derived. The most important fact to recognize is that the whole system of excretory or genital tubules in the Craniate is of coelomic origin, to the point at which they reach the cloaca or its equivalent.

as well as coelomoducts rests on our knowledge of the wide distribution of nephridia among the various phyla of Invertebrata, and especially in such forms as the Phoronida which cannot be very distantly related to the Hemichordata; but most of all is the conclusion borne out by what we now know of the excretory organs of the Acrania.

In 1890 Boveri and Weiss almost simultaneously at Naples discovered that *Amphioxus* possesses along its branchial region paired series of excretory tubules opening into the atrium.<sup>1</sup> Weiss could find no internal opening; but Boveri, who later gave an elaborate and well-illustrated account of the excretory organs (1892), described each tubule as provided with several funnels (with strange 'Fadenzellen' spreading out from them) opening into the longitudinal dorsal or subchordal coelomic chambers. The presence of these alleged funnels was taken to prove their homology with the pronephric funnels of the Craniata. When, however, it was shown (Goodrich, 1902) that no such open funnels are present, that the tubules are only provided with short blind diverticula, and that the 'Fadenzellen' are typical solenocytes projecting from the wall of the excretory canal (Text-fig. 95); and, further, that the canal and solenocytes bear just the same relation to the coelom and its lining epithelium as do those of the pronephridia of adult Polychaeta (the canal being covered by coelomic epithelium, and the solenocytes being exposed to the coelomic fluid (Text-fig. 96)), it became evident that the excretory organs of *Amphioxus* represent the primitive pronephridia of the ancestral form, having nothing to do with the extrusion of genital products and being only secondarily related to the coelomic cavity.<sup>2</sup> We shall see

<sup>1</sup> In the adult one tubule corresponds to each primary gill-slit, and opens at the dorsal end of each tongue bar which divides such slits into two. In this way the segmentation of the tubules agrees with the adult branchiomery. The segmentation of the various systems in *Amphioxus* does not necessarily correspond in the adult. For instance myomeres, gill-slits, and median fin-rays each have their own segmentation. But in ontogeny the primary (undivided) gill-slits appear to arise between the somites and to be intersegmental at first, though this correspondence is lost later owing to differences in relative growth (Willey, 1894).

<sup>2</sup> Without going into unnecessary detail something must be said about

that this conclusion is confirmed by a study of their development.

The paired protonephridium of *Amphioxus* (*Branchiostoma lanceolatum* Pallas) may briefly be described as

the controversy over the presence or absence of open funnels, which has been more fully dealt with elsewhere (Goodrich, 1902, 1909, 1933, 1934). This controversy is not without its humorous side. After the protonephridial character of these organs in *Amphioxus* had been demonstrated (Goodrich, 1902), Boveri (1904) persisted in stating that although solenocytes existed open funnels were present also. Felix (in Hertwig's 'Handbuch', 1904), accepting my description and conclusions, published Boveri's figures 'corrected after Goodrich'; but later, when Boveri had protested, he recanted, and reproduced Boveri's original figures in a general account of the Vertebrate excretory system (1904b). Later (1909) I gave much detailed evidence to show that the wall of the canal to the very extremity of the diverticula from which spring the solenocytes is complete, and that the solenocyte tubes pass through it to reach the lumen. It was also shown that injections into the dorsal coelom do not penetrate into the canals. Moreover, it was mentioned as final proof that in the living nephridium the fluid in the canal under the pressure of a cover-slip could sometimes be seen to dilate the tip of the diverticulum where an opening was said to exist. No doubt the deceptive appearance of an opening is to be attributed to the absence of nuclei in this region of the wall (the nuclei being, so to speak, drawn out with the cell-bodies of the solenocytes), and the relative scarcity of granules rendering this particular region difficult to stain. In 1910 Legros adopted my interpretation.

Franz, who made some valuable contributions to our knowledge of the microscopic anatomy of *Amphioxus*, again attacked the problem in a series of publications (1926, 1927, 1934). While admitting that 'Öffnungen ins Coelom haben die Nephridien zweifellos nicht', he brushed aside the evidence given by me, and attempted to describe the tubules as both open and closed—open because there were holes in the canal wall, closed because these holes were blocked by the bundles of solenocyte tubes! The alleged holes were described and figured by Franz as due to the sudden interruption of the wall and marked by a sharply defined edge—a description totally at variance with my own observations both on living and fixed material. Franz seems to have reached this remarkable conclusion under the influence of the account given by Legros of their development (dealt with later). He also considered that the solenocytes became only secondarily related to the canal. Needless to say that neither Franz nor Legros has ever given even a plausible explanation of how such a mechanism could work, how its phylogenetic stages could have been evolved, or how the theory can be reconciled with what we know of the structure, functioning, and development of solenocyte-bearing nephridia in other

follows: It is situated in the membrane (ligamentum denticulatum) separating atrium from dorsal coelom, and composed of three layers (outer atrial epithelium, inner coelomic epithelium, and layer of connective tissue between). The pore, near the dorsal end of a tongue bar, opens into the atrium at the posterior edge of this bar.<sup>1</sup> The excretory canal has a multicellular wall and intercellular lumen; its cells contain many granules and flagella extend from them towards the pore, sometimes beyond it. The naked cell-body of the solenocyte contains the nucleus and is attached to the wall of the cavity in which it lies. Its slender cylindrical tube passes freely to the canal and pierces its wall, while the flagellum extends into its lumen. The length of the tube varies according to the distance of the cell-body from the canal, it may be nearly 100  $\mu$  in length. It has been estimated that the number of solenocytes in a full-grown animal may be about 100,000, and the total length of solenocyte tube about 5 metres, a not inconsiderable surface for osmotic exchange (Goodrich, 1902).<sup>2</sup>

forms. It must surely be admitted that there is overwhelming evidence that in such protonephridia flame-cells or solenocytes are and must always have been an integral part of the whole organ. As already mentioned Legros (1910) agreed that my description of the adult protonephridium of *Amphioxus* is correct.

The views of Naef will be dealt with when discussing the development, p. 369.

<sup>1</sup> Franz (1926) drew attention to an unfortunate 'slip of the pen' in my description (Goodrich, 1909) where the pore is stated to be on the 'anterior outer surface of the secondary or tongue bar'. He did not notice that in the same paper its position was correctly indicated at the posterior edge of the bar, at the angle where this bar joins the atrial wall in fig. 23, Pl. 14.

<sup>2</sup> To find in a Cephalochordate protonephridia and solenocytes so like those of the polychaete *Phyllodorea paretii* was a surprising fact, but it should now be realized that such organs with some kind of flame-cell occur in almost every Class of Triploblastic Invertebrate. The flame-cells vary much in the different families and genera, and show considerable convergent adaptive resemblances in widely separated groups. The closest likeness to the protonephridium and solenocyte of the Cephalochordate (as seen in *Asymmetron*, Text-fig. 95 A) is perhaps shown by those of the larva of *Phoronis*, and the *Phoronida* would appear to be not improbably related to the Echinodermata and Chordata. Another form possibly also related is *Priapulius*, which also has very similar solenocytes.



TEXT-FIG. 95.

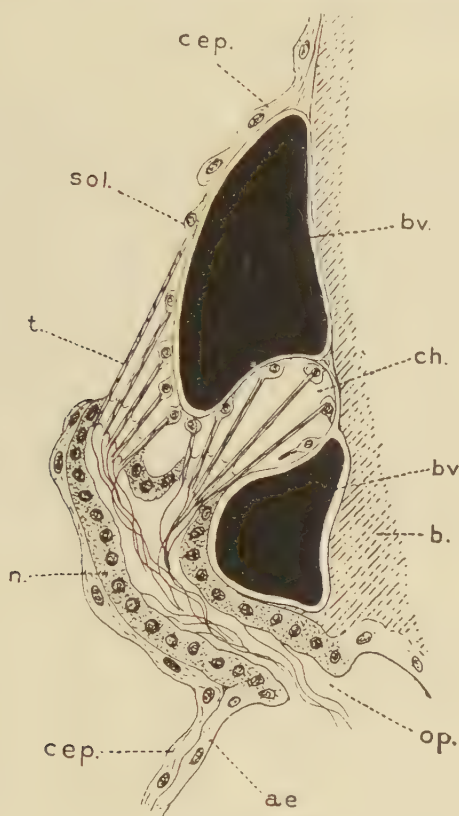
*Branchiostoma lanceolatum*. Left view of dorsal portion of pharynx showing nephridia on inner wall of coelom. *c*, lateral dorsal longitudinal coelom, outer wall removed; *ct*, cut edge of denticulate ligament; *d*, blind diverticulum of nephridial canal, *n*; *p*, nephridiopore; *PB*, primary gill-bar; *SB*, secondary gill-bar (Goodrich, 1933).



TEXT-FIG. 95 A.

Left view of dorsal region of wall of pharynx of *Asymmetron lucazanum*, drawn with camera from a stained preparation; cut edge of denticulate ligament diagrammatic. Lettering as in Text-fig. 95 (Goodrich, 1933).

Such protonephridia extend throughout the pharyngeal region, but dwindle in size towards the posterior end, for it is here that new gill-slits and new nephridia are formed during



TEXT-FIG. 96.

*Branchiostoma lanceolatum*. Diagram of transverse section showing relations of nephridium to neighbouring structures. *ae*, atrial epithelium; *b*, top end of secondary gill-bar; *bv*, blood-vessel; *cep*, coelomic epithelium; *ch*, chamber with solenocytes; *n*, wall of nephridial canal; *op*, nephridiopore; *sol*, solenocyte; *t*, its tube with flagellum (Goodrich, 1909).

growth. In *Asymmetron*, also, they remain small and relatively simple in structure (Text-figs. 95 and 95 A).<sup>1</sup>

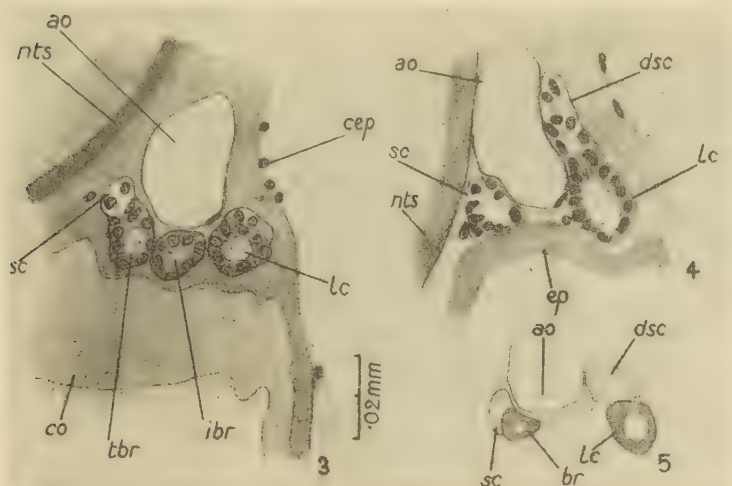
<sup>1</sup> A point of real importance, which unfortunately is not yet settled,

**The Unpaired Protonephridium of Hatschek.**—In addition to the paired nephridia of the branchial region there is in the head region a single organ now known as Hatschek's nephridium. First noticed by Hatschek (1884), it was not till after the solenocytes of the paired organs had been described by me, and the presence of similar cells in Hatschek's nephridium had been described by Goldschmidt (1905), that the protonephridial nature of this unpaired organ was understood (Goodrich, 1909). This relatively large nephridium opens dorsally on the left into the pharyngeal cavity just posteriorly to the velum. Its canal runs forward, above the hood-cavity, along the ventral left side of the notochord, and closely related to the left dorsal aorta (Text-fig. 97). Its blind anterior end extends slightly beyond the level of Hatschek's pit. Along its course are given off irregular short diverticula bearing bunches of solenocytes projecting into special chambers, some situated laterally and some ventrally to the aorta (Goodrich, 1909, 1933, 1934; Legros, 1910).<sup>1</sup>

**Development of Hatschek's Protonephridium.**—In the adult this nephridium runs forward in a space bounded by a connective tissue wall. As Legros (1910) showed, the may here be mentioned. There seems to be no doubt that in *Branchiostoma neapolitanum* the space in which lie the solenocytes is in communication with the coelom owing to the interruption of the coelomic epithelium mentioned above. But Franz (1926) remarks that in *Branchiostoma belcheri* he is inclined to believe that a thin membrane may remain covering the solenocytes, and may shut them off from the coelom. Now, sections of *Asymmetron* seem to show that the coelomic epithelium may partially, if not completely, cover the solenocyte field. If this covering could for certain be shown to be present, it would prove that the whole protonephridium, solenocytes as well as canal, is retro-peritoneal, and help to demonstrate the correctness of my interpretation of its development (p. 369).

<sup>1</sup> Franz (1926, 1927) emphatically denied the presence of these diverticula, but has since corrected his mistake (1934). He still persists, however, in his belief that the wall of the canal is interrupted, the holes being merely blocked by the solenocyte tubes. That the wall is really continuous can more easily be seen in the living larva, where Hatschek's protonephridium is straight (Text-fig. 99), and the tubes can be seen passing through its dorsal wall (Goodrich, 1909, fig. 38, Pl. 15). That the solenocyte tubes pierce the closed wall of the canal in the adult is admitted by Legros (1910).

chambers are the remains of the mid-region (*vésicule intermédiaire*) of the coelomic cavity of the second embryonic somite. Later, in the larva, it becomes closed off both from myocoel above and from splanchnocoel below (Goodrich, 1909; Legros, 1910), and after metamorphosis as solenocytes



TEXT-FIG. 97.

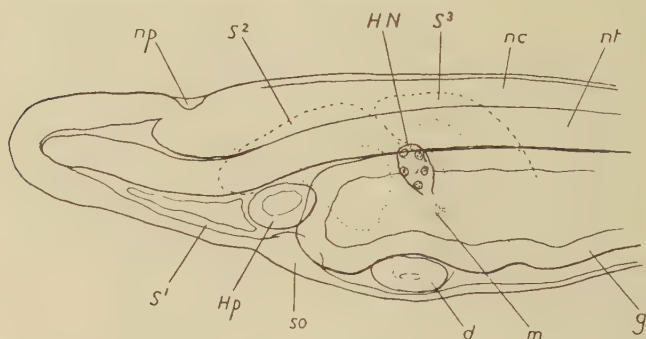
*Branchiostoma lanceolatum*. Transverse sections through Hatschek's nephridium. *ao*, left dorsal aorta; *br*, *ibr*, *tbr*, inner branches of canal; *cep*, coelomic epithelium; *co*, ciliated organ; *dsc*, dorsal solenocyte chamber; *lc*, longitudinal nephridial canal; *nts*, notochordal sheath; *sc*, inner solenocyte chamber (Goodrich, 1933).

become restricted to outgrowing diverticula, the coelomic cavity becomes subdivided into chambers surrounding the solenocytes, and is practically obliterated elsewhere.

According to Legros (1910) the nephridium itself is developed in the early larva (before the mouth is pierced) as a funnel-shaped outgrowth on the left of the coelomic wall of the '*vésicule intermédiaire*' just mentioned. He further alleges that the solenocytes are modified epithelium cells of the coelomic wall which grow tubes towards the funnel, and that

these tubes become involved in the later closure of the funnel opening.<sup>1</sup>

The result of my own observations on the development of Hatschek's nephridium was quite different (Goodrich, 1934). Not only could no funnel-shaped outgrowth of somite 2 be found; but at no stage does the rudiment of the nephridium



TEXT-FIG. 98.

*Branchiostoma lanceolatum*. Left side view of anterior region of thirty-hour larva, showing Hatschek's nephridium, *HN*, above the point, *m*, at which the mouth will become pierced. *S*<sup>1,2,3</sup>, somites; *d*, duct of club-shaped gland; *g*, wall of gut (Goodrich, 1934).

acquire any internal opening. The rudiment can first be identified, at a stage before the buccal diverticulum of the gut has appeared, as one or two cells applied to the endoderm between the posterior wall of somite 2 and the anterior of somite 3. By the time the mouth has become pierced on the left side the rudiment is in the form of a small solid independent mass of cells (Text-fig. 98). It soon acquires a lumen and grows through the endodermal roof of the gut above the mouth to form its pore. The sac then grows forwards along the inner wall of somite 2, the covering coelomic epithelium becomes interrupted, and solenocytes grow out from the nephridial wall (Text-fig. 99). The actual first origin of the nephridial cells could not be traced. It seems to be neither from the ectoderm nor from the endo-

<sup>1</sup> Neither the figures nor the descriptions of these peculiar proceedings are convincing.

derm of the early larva, but the first rudiment is probably set aside in late cleavage or in the embryo as an independent nephridioblast between the two layers. At all events no evidence could be found of its having been derived from the segmented mesoblast.<sup>1</sup>



TEXT-FIG. 99.

*Branchiostoma lanceolatum*. Left side view of anterior end of larva with eleven open 'primary' gill-slits. *Hneph*, Hatschek's nephridium; *neph*, second protonephridium of left adult series (Goodrich, 1930).

**Development of the paired Protonephridia.**—Legros (1909) was the first to study the early development of the paired nephridia of the branchial region. An account of these organs in larvae with about ten to fifteen of the first (future left) series of gill-slits was given a little later (Goodrich, 1909). They were shown to be present at the posterior corner

<sup>1</sup> In early stages Hatschek's nephridium seems to be related to the mouth as the paired nephridia are to the gill-slits. This has been taken as evidence that the mouth is a modified gill-slit. Such a conclusion, however, does not seem to be justified. The original position of the pore is retained in the adult and is not affected by the shifting of the mouth to its definitive position in the middle of the velum.

of each slit as small sacs opening to the exterior at the limit between endoderm and ectoderm of the future atrial wall. As development proceeds each sac migrates with its gill-slit from a ventral to a dorsal position on the left. From the closed inner end of the sac extends a bunch of solenocytes; some of these, with very long tubes, come to spread over the left side of the aorta. Owing to various difficulties the first origin of these organs of the left series could not be made out.

The development of the protonephridia related to the gill-slits of the right side has been described by Legros (1909) and myself (Goodrich, 1934).<sup>1</sup>

According to Legros (1909) the first rudiment of the nephridium appears as a short longitudinal fold of the coelomic epithelium applied to the pharyngeal wall, just above the middle of the simple endodermal thickening representing the beginning of the gill-slit. The fold is said to close over from behind forwards to form a cul-de-sac open to the dorsal coelom anteriorly, and having its outer surface covered by coelomic epithelium. When the thin-walled gill-pouch develops the blind end of the canal fuses with it, and then opens into the endodermal gill-pouch. Meanwhile, coelomic epithelium cells near the open funnel become transformed into solenocytes. Those nearest the opening develop solenocyte tubes which are inserted into its inner lip; those farthest from the opening become inserted into its outer lip.<sup>2</sup>

<sup>1</sup> Legros (1909) gave a very careful and accurate account of the development of the right series of gill-slits (previously dealt with by Willey, 1891) showing that from the centre of each endodermal thickening on the inner wall of the pharynx a small thin-walled outgrowing pouch develops, which meets the upgrowing ectodermal atrial wall, and so forms a thin gill-membrane or diaphragm. At this point the gill-slit is pierced in such a way that the endodermal pouch contributes a small dorsal portion of the atrial lining. He further showed that the nephridiopore is first situated in this endodermal area, and indeed opens into the pouch before the slit is pierced. With all the above-mentioned observations I fully agree. Nevertheless, it would seem that in the adult, owing to encroachment of atrial ectoderm, the nephridiopore is at the meeting-point of the two layers (as also held by Franz).

<sup>2</sup> This account was founded chiefly on sections of the first right gill-slit, which develops rather later than the more posterior slits and does not

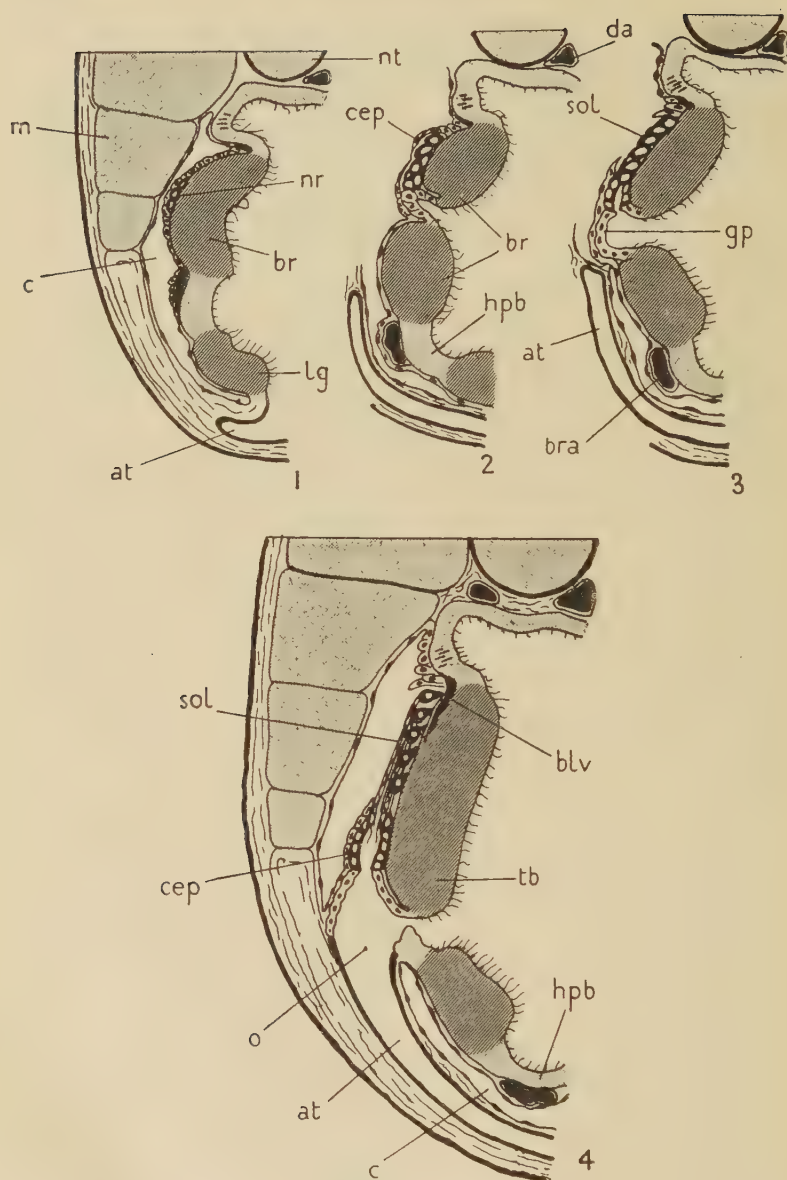
The alleged origin of solenocytes from epithelial cells distinct from the nephridial rudiment, and the later connexion of their tubes with the lumen of the canal by means of the lips of an open funnel which is subsequently closed by a definite wall (for Legros, 1910, admitted that my description of the adult protonephridium was correct)—these are conclusions which could only be accepted on the very strongest evidence (see also footnote, p. 372).

My own observations (Goodrich, 1934) on the development of the nephridia related to the right series of gill-slits do not agree with the results of Legros concerning (a) the first origin of the rudiment, (b) the presence at any stage of an open funnel, and (c) the origin of the solenocytes.

Briefly my results are as follows: At an early stage, when the gill-slit is represented by a mere thickening of endoderm without central gill-pouch, the nephridial rudiment is present as a group of a few cells between outer coelomic epithelium and inner endoderm, and independent of each of these layers (Text-fig. 100, 1, 2). As this plate of cells extends dorsally and develops into a more ventral canal region and more dorsal and peripheral region composed of the future solenocytes, the covering of coelomic cells becomes stretched and broken so that the solenocytes become exposed to the coelomic fluid (Text-fig. 100, 3). The solenocytes remain in continuity with the canal by means of their tubes. Meanwhile, the gill-pouch grows out from the middle of the gill thickening, the nephridial rudiment fuses with it, and finally opens into it. Later still, when the gill opening has been pierced the nephridiopore is found near the posterior edge of the developing tongue bar, while the solenocytes are spread over the expanding solenocyte field (Text-fig. 100, 4). At no time does the canal open internally.<sup>1</sup>

become subdivided by a tongue bar. But Legros considered that the more posterior nephridia are developed in the same way as the first.

<sup>1</sup> Recently Naef (1938) has given an account of the development of the nephridia which agrees neither with my own nor with that of Legros. According to Naef, whose illustrations are merely diagrammatic, the nephridium arises as a proliferation inwards of the coelomic epithelium covering the right endodermal gill thickening. These inner cells form the canal, which opens directly into the pharyngeal cavity through the middle



TEXT-FIG. 100.

The very first origin of the nephridial rudiment is more difficult to determine. In earlier larval stages, when the right gill thickening is scarcely marked, one or two cells may be found in the same place as the plate of cells described above and occupying the same position between mesoderm and endoderm. Although the complete series of stages between one such cell and the plate could not be traced with certainty, there is good reason to believe that the whole nephridial rudiment arises from a single cell or nephridioblast visible even before the appearance of the gill thickening. It was inferred that these nephridioblasts are set apart at the posterior end of the growing embryo at a very early stage and possibly as so-called ectomeso-

of the thickening. The base of this canal enlarges into a 'vestibulum', and this later fuses with the atrial wall and opens into the atrium. Thus, the nephridiopore becomes the inner gill-opening, and epithelium of coelomic origin lines the gill-slit and contributes to the dorsal wall of the atrium! This extraordinary conclusion is difficult to explain except on the supposition that Naef has entirely missed the development of the endodermal gill-pouch so carefully traced by Legros (see footnote, p. 368), whose results were confirmed by me. For according to Naef our gill-pouch is part of the nephridial canal!

For the rest, he finds no internal opening to the nephridial canal, and believes the solenocytes to be modified cells of the coelomic epithelium. It may be remarked that his diagram of the first stage (proliferation?) shown in his Fig. 3*a*, p. 246, might well represent the early retroperitoneal rudiment (compare Text-fig. 100, 1).

#### TEXT-FIG. 100.

*Branchiostoma lanceolatum*. Diagrams illustrating four stages in development of paired protonephridia as shown in transverse sections of developing right gill-slits of larva. *at*, atrium beginning in 1 and completed in 4; *blv*, blood-vessel; *br*, *br*, right gill-thickening; *bra*, ventral aorta; *gp*, endodermal gill-pouch; *hpb*, mid-ventral hypobranchial band; *lg*, edge of left gill opening; *m*, myomere; *nr*, nephridial rudiment (with white nuclei); *nt*, notochord; *o*, opening of right gill-slit into atrium; *sol*, solenocyte; *tb*, tongue bar. 1, Stage II, small protonephridial rudiment of few cells covered over by coelomic epithelium. 2, Stage III, growing rudiment still covered by stretched coelomic epithelium cells. 3, Stage IV, young solenocytes uncovered, nephridial canal fused with gill-pouch. 4, Stage V, solenocytes fully formed, atrium has grown up on right side, fused with and opened into gill-pouch into which protonephridium opens above (Goodrich, 1934).

dermal cells. This would be in accordance with what we know of the origin of the protonephridia of other forms, such as *Phoronis* and various Annelids and Molluscs.<sup>1</sup>

From the account given above it may be concluded that the excretory organs of the Acrania are typical protonephridia, which function as such throughout life, and have been inherited from a primitive invertebrate ancestor.

But, since there is good reason to believe that this ancestor must have been provided with segmental coelomoducts as well, it may be asked whether any traces of these genital ducts occur in the Acrania. All Acrania living at the present day are highly specialized, and the reduction of the genital ducts seems to have been one of the main results of this specialization. It may well be related to the development of the characteristic atrium and the proximity of the gonads to its wall. In this case the germ-cells can easily escape into the atrium and so to the exterior by the atriopore, and tubular ducts are no longer necessary.

The gonad is enclosed in a special chamber of the coelom applied to the atrial wall, and here separated from the atrial epithelium by a layer of connective tissue. The passage of the germ-cells is not effected by the irregular rupture of this wall, but takes place at a definite point—the centre of a thickening known as the cicatrice (*Narbe* of German authors). It has been described by Burckardt, 1900; Neidert and Leider, 1903; Zarnick, 1905; and Cerfontaine, 1906. Its covering of coelomic epithelium becomes columnar, and radiating apparently contractile fibres appear in the middle layer. This cicatrice may well represent a vestigial coelomoduct and deserves further study.<sup>2</sup>

<sup>1</sup> Legros (1910, p. 582) rightly pointed out an error in my paper of 1909, where it is stated (p. 194) that an examination of his sections had convinced me that in the earliest stages 'the whole rudiment of the nephridium and solenocytes lies enclosed between the coelomic epithelium and the atrial wall'. The statement should, of course, have read 'between the coelomic epith. and the pharyngeal wall', since at these stages the ectodermal atrial wall has not reached the region of the rudiment (Text-fig. 100, 4).

<sup>2</sup> The reduction of coelomoducts is by no means unknown in other forms. In various Annelids they not only may fail to develop at all in sterile segments, but in the formation of nephromixia may often be reduced

When Boveri (1892) discovered the excretory organs of *Amphioxus* he concluded that they were homologous with the pronephric tubules of Craniata, and that the atrium into which they open represented the longitudinal pronephric duct. He further maintained that the gonadial coelomic chambers of *Amphioxus* were the homologues of the craniate mesonephric tubules. As explained above, the first theory had to be abandoned when it was shown that the excretory organs of Acrania are protonephridia (Goodrich, 1902, 1909, 1930, 1934). But in Boveri's second theory there is probably an element of truth, for the cicatrices just described may possibly be much reduced vestiges of the ancestral series of segmental genital coelomoducts.

We thus reach the final conclusion with regard to Vertebrata: that, while in the Acrania the protonephridia are well developed and the coelomoducts are vestigial, in the Craniata, on the contrary, the coelomoducts are well developed and have become mostly excretory, and the protonephridia have apparently been altogether lost.<sup>1</sup>

#### GENERAL CONCLUSION.

Looking back on the contributions made since 1895 to the study of genital ducts and nephridia of the Metazoa Triploblastica we may conclude that the foundations of the generalization put forward then (Goodrich, 1895): that there can be distinguished two series of originally quite independent organs—the excretory nephridia, and the primitively genital coelomoducts, which can both be traced throughout the main groups from the lowest to the highest—has been greatly strengthened by the discovery of many new facts extending and completing the evidence. For instance, whereas in 1895 protonephridia

to mere funnels with little or no tubular canal. In the smaller Oligochaeta they may be reduced to little more than 'pores' in the female segments.

<sup>1</sup> There are obvious objections to van Wijhe's suggestion that the thymus represents the modified remnant of the excretory organs of *Amphioxus*, and it has not been generally accepted chiefly because according to current doctrine the thymus is developed from the endoderm.

were known only in Platyhelminia, Nemertina, Gastrotricha, Rotifera, Endoprocta, a few Archiannelida, and the larvae of some Annelida and Mollusca, they are now known to occur not only in the larva of Phoronida but also in the adult of Kinorhyncha, Acanthocephala, Priapulida, and even in such an undoubted vertebrate as *Amphioxus*.

Moreover, while many authors still doubted the homology of the so-called larval 'head-kidneys' of Annelids and Molluscs with the more typical nephridia (metanephridia), this doubt has now been dispelled by the discovery of protonephridia throughout the trunk segments of many Polychaeta. Further, the confusion, brought about by the failure to distinguish in Annelids between true nephridia (whether protonephridia or metanephridia) of exclusively excretory function and compound organs with wide funnels capable of serving as genital ducts as well, was cleared up when the existence of nephromixia was demonstrated. These compound organs, found for certain only among Polychaeta, are formed by the grafting of the coelomoduct on to the nephridial canal so that the genital products can pass through that canal to the exterior. Such a combination is clearly secondary, and no doubt nephridia and coelomoducts were originally separate as they still are in the Capitellidae and many other Annelida, and in many lower forms as well.

All these facts lead to the conclusion that excretory nephridia must have appeared early in the phylogeny of the Triploblastica, must indeed have been present in the form of protonephridia in the ancestor of all the known Phyla even before the development of a coelomic body-cavity.

Such primitive protonephridia, concerned with the elimination of waste products and the regulation of the water content of the tissues, must from the first have opened to the exterior; and with regard to their embryonic origin, and in spite of the unfortunately scanty evidence of the exact mode of their early development, it is now clear that they always originate from relatively superficial cells and grow inwards. That is to say the protonephridia are of ectodermal or ectomesodermal origin. Conclusive evidence for this has been found especially in Annelids, Molluscs, and Phoronis. Primitively they have

nothing to do with a coelom, and it is only when a coelomic body-cavity appears that they may come into secondary relation with it.

An important point is that it has now been shown that the whole nephridium (whether protonephridium or metanephridium) is developed from a single primary rudiment, except in some cases for a small contribution from the ectoderm at the nephridiopore. Flame-cells, solenocytes, or nephridiostome, as well as excretory canal, all come from this one rudiment. The rudiment can generally first be distinguished in Annelids as a conspicuous large cell, the nephridioblast. The characteristic disposition of a nephridium in a segmented Annelid, with nephridiopore in one segment and inner end passing through a septum into the coelom of the next segment in front, is due to the nephridioblast taking up an intersegmental position between two successive coelomesoblastic somites.

The coelomoducts, on the other hand, are always primarily related to the paired genital sacs (or their homologues the paired coelomic somites) where the germ-cells undergo development. They always develop centrifugally as outgrowths from the wall of these sacs. They acquire their opening by fusing with and piercing the ectoderm, and serve to conduct the genital products to the exterior (or they may do this by forming compound nephromixia in combination with the nephridia).

Some such ducts must necessarily have been present in the common ancestor of all Triploblastica. The coelomoducts retain their essential structure throughout the various Phyla, even when the genital sacs expand to form an extensive coelom. But a well-defined funnel-like coelomostome may be differentiated at the inner end, and more or less complex accessory glands and copulatory organs may be added at the external pore from the ectoderm and body-wall tissues.

Such in brief appears to have been the fundamental structure of the ancestor of the Metazoa Triploblastica as regards nephridia and coelomoducts. It can be followed throughout the various Phyla in spite of the many modifications and specializations arising in the course of phylogeny. Some of the more interesting of these modifications may now be mentioned.

The lower forms, such as the *Platyhelminia*, scarcely depart from the primitive plan. In them the protonephridia appear early, persist and continue to grow, and may acquire numerous external pores, while the branches of the canal system may spread in the parenchyma and develop new flame-cells. The chief specializations of the gonadial sacs, which may also branch and spread, are related to the differentiation of some branches into yolk-glands, testes, and ovaries, the coming together of the coelomoducts to open by a common ventral pore, and the development of a complex copulatory apparatus. In the *Rotifera*, where the parenchyma is to a great extent replaced by a space containing fluid, the protonephridia come into relation with it. Similarly, in the *Nemertina*, where a blood-vascular system appears, the flame-cells may gather near and even project into the lateral vessel. The great elongation of the body in *Nemertines* favours the tendency, already seen in *Platyhelminia*, for the subdivision or repetition of organs. This leads to the breaking up on each side of the single protonephridium into a series of separate organs opening independently to the exterior. In the same way series of genital sacs are formed, each sac with an incipient coelomic cavity and a coelomoduct. Posteriorly some of these sacs may remain sterile and form no duct, thus foreshadowing what so often occurs in the true *Coelomata* both anteriorly and posteriorly.

The regular repetition of both nephridia and coelomoducts may well have produced the *Annelid* type of metameric segmentation with a pair of each to every segment. It may here be mentioned that this regular disposition of the nephridia may be disturbed secondarily by the subdivision of each nephridium into several independent organs, both in *Polychaeta* (*Capitellidae*) and in *Oligochaeta*. In the latter Class this process leads to remarkable divergent specializations of the resulting nephridia, some of which come to open not to the exterior but into the alimentary canal. Rarely anastomosing networks may be formed in the body-wall between neighbouring nephridia in *Hirudinea* and *Oligochaeta*.

It should be noticed that, speaking generally, excretion being necessary so soon as an animal becomes active, nephridia tend

to appear early in development and persist throughout life. Coelomoducts, on the other hand, may appear late and reach full development only at sexual maturity.

When in the higher groups (according to the Gonocoele Theory) the genital sacs expand into coelomic sacs filled with fluid and acquire new functions—a modification which has probably developed independently in several Phyla—an important new specialization may arise: it is the assumption by the coelomoduct of the excretory function.

It follows that the nephridium may be more or less completely superseded, or relegated to the embryonic or larval stages, to be replaced later by a new type of excretory organ derived from the coelom. This new coelomoducal kidney, being adapted to the same function, may come to resemble closely the old organ it has replaced, and consequently has often been mistaken for it.

The substitution of coelomoducts for nephridia has taken place in the Arthropoda (which have doubtless been derived from Annelid-like ancestors), in which Phylum only the Crustacea appear possibly to have retained a trace of the nephridial series. It has also happened in the Mollusca, though here the nephridium may still occur as a larval protonephridium before the coelom has developed. In several other Phyla also the coelomoducts alone seem to remain in the adult, such as the Ectoprocta, Sipunculida, Echinodermata, Enteropneusta, Tunicata, and Craniata.

This assumption by the coelomoducts of the excretory function often leads in segmented forms to a division of labour among them; the majority, and generally the more anterior, being devoted entirely to excretion; while a few, generally more posterior, retain their original role of genital ducts. The same differentiation may occur among the nephromixia of the Polychaeta.

Other modifications are the combination of successive genital coelomoducts to open by a common pore backwards in Oligochaeta and Craniata, or forwards as in Hirudinea; and the subdivision of a coelomoduct into an excretory and a genital duct found in the Mollusca. Finally, the coelomoducts in certain Polychaeta, whether they are independent or in association

with nephridia to form nephromixia, may become reduced to the condition of mere coelomostomes which cease to open to the exterior and help to build up a cilio-phagocytal organ. In such worms the genital products escape by rupture of the body-wall.

Great as may be the changes in structure and function undergone in the various Phyla by nephridia and coelomoducts, they generally can be clearly distinguished from each other by a careful study of their comparative anatomy and embryology.

#### SUMMARY.

In 1895 a general review of the morphology of nephridia and genital ducts, and their relation to each other and to the coelom, was published by me (Goodrich, 1895). The present paper is a similar review of the work done since that date on these organs throughout the Metazoa Triploblastica. It is shown that a great many newly discovered facts support the conclusions put forward in 1895, notably the conclusion that two different organs of independent origin—genital ducts and excretory nephridia—can be traced through the various Phyla of Triploblastica. The Gonocoel theory is accepted as the best explanation of the origin of the coelom. In all the various groups coelomoducts, primitively acting as genital ducts, are shown to be derived from the epithelial wall of the gonadial sac, or its derivative the coelomic sac, as centrifugal outgrowths which meet the ectoderm and come to open to the exterior; whereas the excretory nephridia are to be derived from superficial rudiments, often in the form of nephridioblasts, which develop centripetally, and give rise to the whole nephridium whether protonephridial or metanephridial. The nephridial rudiments are not developed from the coelomesoblast, but are either of ectodermal or of ectomesodermal origin. The coelomoducts are always of coelomesoblastic origin. In some Polychaeta (and possibly some Archiannelida) nephridium and coelomoduct may combine to form a nephromixium of both excretory and genital function. In many groups some of the coelomoducts may secondarily acquire an excretory function. In such groups nephridia may disappear, or be no longer developed; provisional larval

nephridia may, however, persist until the excretory coelomoducts are developed.

Suggestions for the improvement of the nomenclature of these organs and their specialized modifications are made (pp. 117, 119). Incidentally many new unpublished observations on their structure and development are recorded. More particularly may be mentioned the early development and morphological relations of the nephridioblast in *Tubifex* (p. 271).

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The titles of many of the publications in this list have been shortened as follows:

A.A. = Anatomischer Anzeiger.

A. z. I. W. = Arbeit. zool. Inst. Wien.

J.M. = Journal of Morphology.

Ph. Tr. R. S. = Philosophical Transactions of the Royal Society, London.

P.Z.S. = Proceedings of the Zoological Society, London.

Q.J.M.S. = Quarterly Journal of Microscopical Science.

Z.J.A. = Zoologischer Jahrbücher Abt. f. Anatomie.

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